MAMMALIAN DIVERSITY AND MATSES ETHNOMAMMALOGY IN AMAZONIAN PERU PART 5. RODENTS

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ABSTRACT

In this report, the fifth and last of our monographic series on mammalian diversity and ethnomammalogy in the Yavarí-Ucayali interfluvial region of northeastern Peru, we document the local occurrence of 40 species of rodents, including 5 sciurids, 17 cricetids, 1 caviid, 1 cuniculid, 2 dasyproctids, 1 dinomyid, 2 erethizontids, and 11 echimyids. The following substantive taxonomic results, among others, are reported: (1) We discuss current issues of sciurid classification and treat all New World tree squirrels (Sciurini), except North American *Tamiasciurus*, as members of the genus *Sciurus*; the proposed subgeneric classification is monophyletic, and it conserves longstanding binomial usage for most species. (2) We describe a new species of squirrel, *Sciurus* (*Hadrosciurus*) *pachecoi*, which had previously been identified as a distinct lineage by molecular analyses. (3) We discuss the nominal taxa currently synonymized with *S.* (*H.*) *pyrrhinus* and comment on the application of names to phenotypes and mitochondrial haplogroups. (4) The currently accepted type locality of *S.* (*H.*) *spadiceus* (Cuiabá) cannot be correct; instead, documentary evidence suggests that the holotype must have been collected near Santarém. (5) *Sciurus flaviventer* appears to be the only valid species of *Microsciurus* (sensu lato) that occurs in the Amazonian lowlands; Amazonian records of taxa previously reported in the literature as *M. sabanillae* and *M.* "species 2" appear to be based on erroneous geographic coordinates and unexplained genotype/phenotype discordance, respectively. (6) We discuss and illustrate the diagnostic morphological characters of *Nectomys apicalis* and *N. rattus*, which have broadly overlapping distributions in northern Peru. (7) We analyze cytochrome *b* sequence data from 143 specimens of *Oecomys* from western Amazonia and summarize evidence for multiple unnamed lineages; of these, three from the Yavarí-Ucayali interfluve are described as new species. (8) We question the recognition of *O. tapajinus* as a species distinct from *O. roberti* due to the lack of unambiguously diagnostic characters and the doubtful identity of the holotype of *tapajinus*. (9) We confirm sympatry between two species of *Scolomys* and provide revised diagnostic criteria for *S. melanops* and *S. ucayalensis*. (10) We report the only specimen of *Dinomys branickii* accompanied by definite locality data from Loreto department. (11) *Proechimys quadruplicatus* and *P. steerei*, closely related species previously thought to occur on opposite banks of the Peruvian Amazon, are both present in the Yavarí-Ucayali interfluve; diagnostic characters are tabulated for the six species of *Proechimys* now known to occur in our region.

Despite intensive and methodologically complementary faunal-sampling efforts, our rodent inventory is probably incomplete; at least four additional species could be expected to occur in our region based on geographic range data. If all four do occur there, then our inventory is about 90% complete. Documented sympatric species richness at intensively sampled sites in our region is substantially less than the regional total, but because of methodological omissions, no site is believed to have been completely inventoried for rodents. In the absence of known barriers to mammalian dispersal within the Yavarí-Ucayali interfluve, however, local (sympatric) species richness is probably constrained only by habitat availability.

Matses knowledge of rodents is richly detailed for primary game species (*Cuniculus paca* and *Dasyprocta fuliginosa*) but is less detailed for less culturally important subsets of the fauna. As previously documented for other mammals (e.g., primates, xenarthrans, and ungulates), important game species are known by multiple names (including synonyms and hyponyms), whereas less culturally important but still salient species (e.g., squirrels) have single names, and many inconspicuous (e.g., small, nocturnal, and morphologically indistinguishable) species do not have unique identifiers.

With the rodents treated in this report, the mammalian fauna of the Yavarí-Ucayali interfluve is now known to include at least 201 species, but >20 additional species (mostly bats) could still be expected in the region based on geographic range data. Despite the probable incompleteness of our inventory, the Yavarí-Ucayali interfluve is the only part of western Amazonia with an extensively documented mammal fauna. Therefore, the completion of this monographic series provides a unique taxonomic resource for urgently needed mammalogical research in this ecologically intact but increasingly vulnerable region.

INTRODUCTION

This report is the fifth and final installment of a monographic series on mammalian diversity and ethnomammalogy in a sparsely inhabited region of lowland rainforest between the Yavarí and Ucayali rivers in northeastern Peru (figs. 1, 2). Like others in this series, the present monograph is based on specimens and observations collected in the region over many decades, and on ethnobiological research with the Matses, a Panoan-speaking group of indigenous Amazonians with intact traditional knowledge of the local fauna. The primary objectives of these monographs are to document the species richness of the regional mammalian fauna through taxonomic analysis of collected specimens, and to assess the extent of Matses knowledge of mammalian natural history based on recorded interviews and other ethnographic methods.

Our introductory report (Voss and Fleck, 2011) summarized current knowledge about the physical geography, climate, and vegetation of the Yavarí-Ucayali interfluve, provided background information about the indigenous cultures of the region, and analyzed taxonomic and ethnographic data on primates. A second report (Voss and Fleck, 2017) provided equivalent taxonomic and ethnographic treatments of the larger mammals (Xenarthra, Carnivora, Perissodactyla, Artiodactyla, Sirenia); a third (Voss et al., 2019) treated the regional marsupial fauna (Didelphimorphia); and a fourth (Velazco et al., 2021) was focused on bats (Chiroptera). In this, our last report, we concern ourselves with rodents, which include some of the most taxonomically neglected clades of Amazonian mammals.

South American rodent faunas comprise the descendants of ancient endemic radiations of caviomorphs (capybaras, agoutis, porcupines, spiny rats, etc.) together with more recent radiations of squirrels and cricetids (Maestri and Patterson, 2016; Abreu et al., 2020a). These species vary greatly in size (from about 10 grams to almost 80 kilograms) and they have disparate ecobehavioral traits: some are terrestrial whereas others are arboreal or semiaquatic; many are granivores, whereas others eat fruit, leaves, or bark; most are nocturnal, but a few are strictly diurnal (Emmons, 1997; Patton et al., 2015). Such behavioral diversity makes it difficult to inventory Amazonian rodent faunas, with the result that taxonomically comprehensive faunal surveys are few and far between. Additionally, many morphologically cryptic species belong to unrevised genera, so even with specimens in hand it can be challenging to identify sympatric congeners.

The taxonomic portions of this report are primarily based on morphological comparisons and craniodental measurement data supplemented by DNA sequence analyses of problematic taxa. Our results include descriptions of four new species and numerous advances in our understanding of the diagnostic traits and geographic distributions of other, previously described taxa. We conclude with summary comments on the regional rodent fauna and on Matses rodent nomenclature and ethnozoology.

MATERIALS AND METHODS

Taxonomic Methods

SOURCE OF MATERIAL: The specimens examined for this report and others mentioned in our text are preserved in the following collections: AMNH (American Museum of Natural History, New York), BMNH (Natural History Museum, London), FMNH (Field Museum, Chicago), INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus), KU (University of Kansas Biodiversity Research Center, Lawrence), LSUMZ (Louisiana State University Museum of Natural Science, Baton Rouge), MCZ (Museum of Comparative Zoology, Harvard University, Cambridge), MHNG (Muséum d'Histoire Naturelle de Genève, Geneva), MNHN (Muséum National d'Histoire Naturelle, Paris), MSB (Museum of Southwestern Biology, University of New Mexico, Albuquerque), MUSA (Museo de Historia Natural de la Uni-
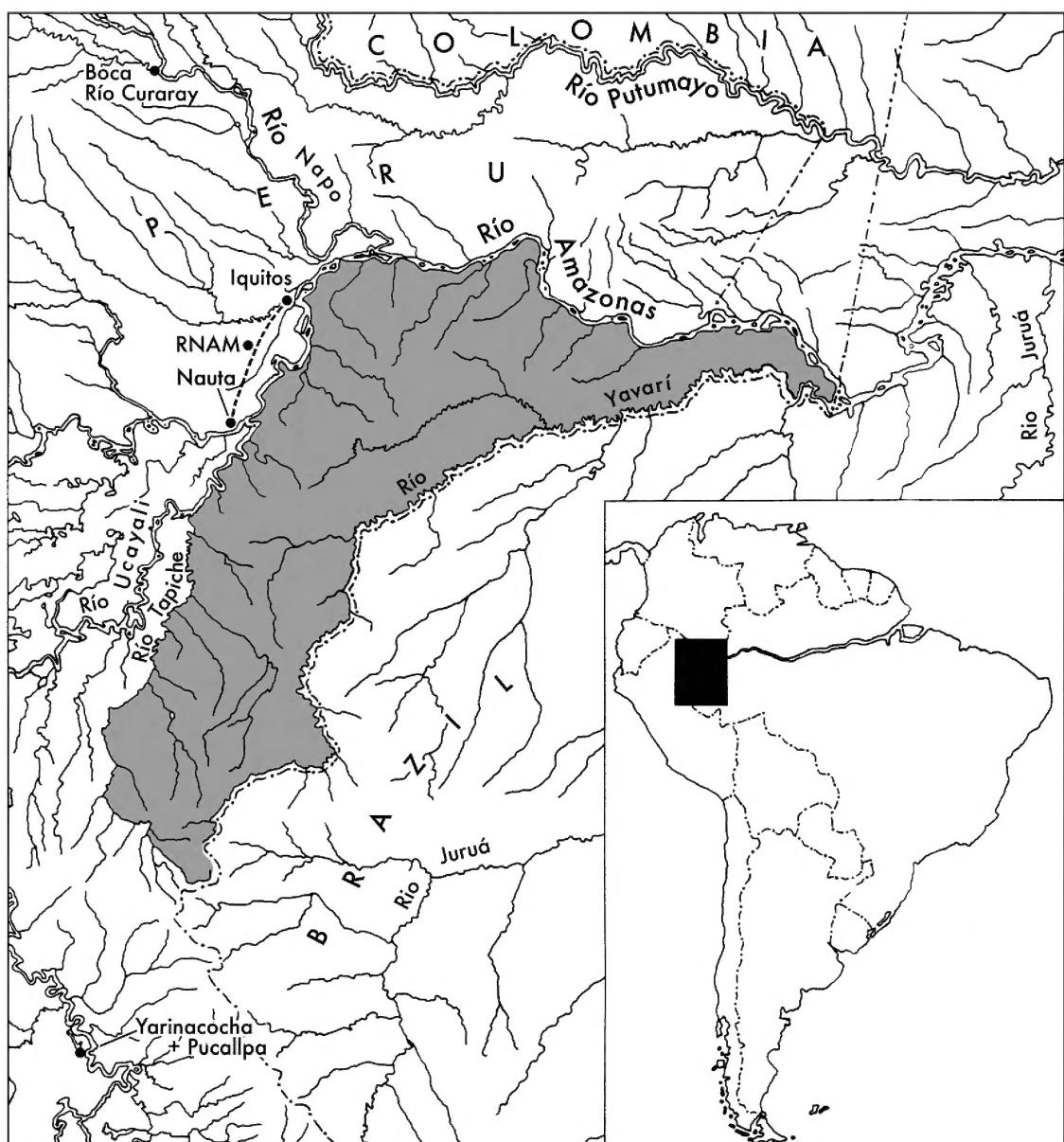
FIG. 1. The Yavarí-Ucayali interfluve (shaded) in relation to surrounding geographic features of western Amazonia. A dashed line marks the highway from Iquitos to Nauta on the left (north) bank of the Amazon. RNAM = Reserva Nacional Allpahuayo-Mishana (site of the Estación Biológica Allpahuayo).

versidad Nacional de San Agustín de Arequipa, Arequipa), MUSM (Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima), MVZ (Museum of Vertebrate Zoology, University of California, Berkeley), RMNH (Rijksmuseum van Natuurlijke Historie, Leiden), ROM (Royal Ontario Museum, Toronto), TTU (Museum of Texas Tech University, Lubbock), ZMB (Museum für Naturkunde, Berlin), ZMMU (Zoological Museum of Moscow University, Moscow), ZSM (Zoologische Staatsammlung München, Munich).
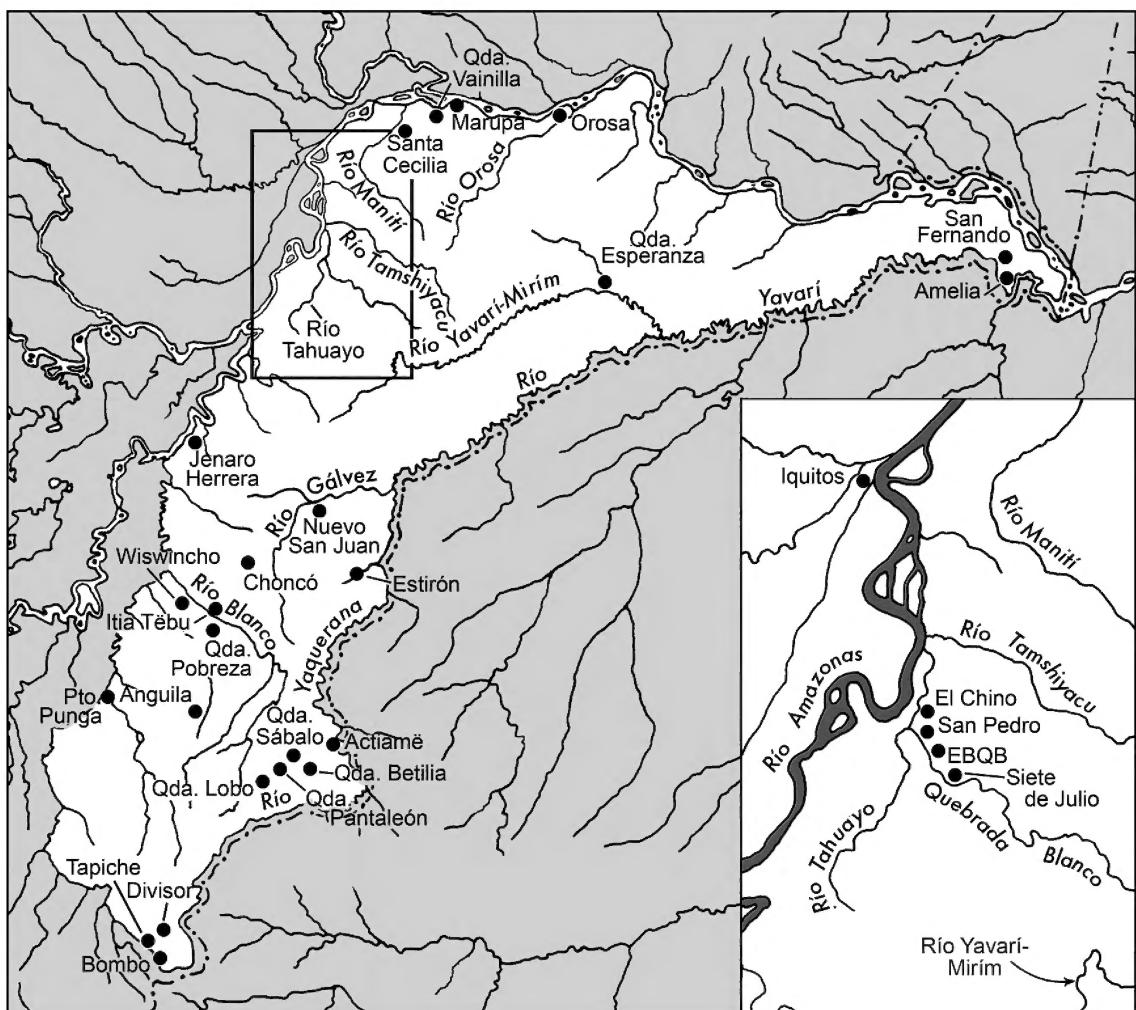
FIG. 2. Faunal inventory sites and other collecting localities within the Yavarí-Ucayali interfluve (see appendix 1 for geographic coordinates and other information). EBQB = Estación Biológica Quebrada Blanco.

Measurements and descriptive statistics: Except as noted, external measurements are those taken in the field by collectors using the standard American protocol (Hall, 1962). We transcribed total length (nose to fleshy tail-tip, TL) and length of tail (basal flexure to fleshy tip, LT) from specimen labels or field notes, and we computed head-and-body length (HBL) by subtracting LT from TL. We also transcribed length of hind foot (heel to tip of longest claw, HF), length of ear (from notch, Ear), and weight from specimen labels or field notes, but we sometimes remeasured HF on skins and fluid-preserved specimens to check the accuracy of values recorded by collectors, and we used our values whenever discrepancies were found. All external measurements are reported to the nearest millimeter (mm), and all weights are reported to the nearest gram (g).

We measured skulls and teeth with digital calipers to the nearest 0.01 mm, and we used unrounded values to compute descriptive statistics, but values reported in our tables and text are rounded to the nearest 0.1 mm (the smallest

decimal fraction of a millimeter that is consistently obtainable with repeated caliper measurements). We used different sets of craniodental measurements for squirrels, cricetids, and caviomorphs as defined and illustrated in the introductory accounts for those taxa.

We computed standard descriptive statistics in Excel. For most series of specimens we tabulate the mean, standard deviation, observed range (minimum–maximum) and sample size. Sample estimates of central tendency and dispersion provided without explanation in our text consist of the mean plus or minus one standard deviation.

AGE CRITERIA: Except as noted, all measurements were recorded from adult specimens as judged by craniodental maturity. The criteria that we used to judge craniodental maturity in squirrels, cricetids, and caviomorphs are defined in the accounts that follow.

MOLECULAR SEQUENCING AND PHYLOGENETIC ANALYSIS: To supplement our morphological data for species of two uniquely difficult genera—*Oecomys* and *Proechimys*—we sequenced and analyzed fragments of the mitochondrial gene encoding cytochrome *b* (CYTB). We extracted DNA from fresh tissues of *Oecomys* and from dried terminal phalanges clipped from skins of *Proechimys* using DNeasy Blood and Tissue Kits (Qiagen). We extracted DNA from the dried tissue samples using the same wash and extraction protocol and in the same dedicated historic DNA lab previously described by Giarla and Voss (2020). For fresh-tissue extracts of *Oecomys* DNA, we amplified the first 801 bp of CYTB using published primers, but we designed custom primers to sequence overlapping 200–300 bp fragments from the *Proechimys* extracts (appendix 2). Custom primers were designed using Primer3 (Untergasser et al., 2012), based on conserved regions of an alignment of two *Proechimys* mitochondrial genome sequences obtained from GenBank: NC039550 (*P. steerei*) and NC039370 (*P. quadruplicatus*). PCR reactions for fresh-tissue and dry-tissue samples were set up in separate facilities to avoid

cross contamination, but they were carried out using similar reaction conditions and thermocycler protocols. PCR reactions included 13 μl of GoTaq polymerase (Promega), 9 μl water, 1 μl of each primer, and 1 μl of DNA for a 25 μl mixture. The thermocycler protocol began with an initial denaturation step of 95° C for 2 min., followed by 40 cycles of denaturation at 95° (30 s), annealing at 50° (30 s), and extension at 72° (1 min.), followed by a final extension for 5 min. at 72°. All PCR reactions included a negative control to rule out reagent contamination. PCR products were run on a 1% agarose gel to verify that the amplified fragment was the expected size. Successful PCR products were enzymatically purified using Exo-SAP-IT (Thermo-Fisher) and sent to GeneWiz (South Plainfield, NJ) for Sanger sequencing.

Sequence chromatograms were trimmed, assessed for quality, and assembled in Geneious R9 (Biomatters). Consensus sequences were then combined with other CYTB sequences from GenBank (including outgroups; see below) and aligned using MAFFT 7.309 (Katoh and Standley, 2013); both alignments (one each for the *Oecomys* and *Proechimys* datasets) were examined by eye to check for premature stop codons or other potential errors. Intra- and interspecific p-distances were estimated in MEGA 11 (Tamura et al., 2021). Both datasets were subjected to the same maximum likelihood (ML) phylogenetic protocol in IQ-TREE 2.1.3 (Minh et al., 2020). First, each dataset was divided into three subsets according to codon position. The best-fitting nucleotide substitution models and partitioning schemes were then identified using ModelFinder (Kalyaanamoorthy et al., 2017). For *Oecomys*, the best-fitting models for codon positions 1–3 were TIMe+I+G4, F81+F+I, and TIM3+F+I+G4, respectively. For *Proechimys*, the best fitting model for codon positions 1 and 2 was HKY+F+I, and the best-fitting model for position 3 was TIM2+F+G4.

We inferred ML trees from these sequence datasets using default settings in IQ-TREE, and we estimated branch support via 1000 ultrafast

bootstrap replicates. For the *Oecomys* analysis, we used exemplar sequences from GenBank of *Euryoryzomys russatus* (ON160918), *Hylaeamys megacephalus* (KP778447), *Nephelomys devius* (MN547729), and *Transandinomys talamancae* (KP778202) as outgroups (to test generic monophyly), and we rooted the tree on *Sigmodon hispidus* (EU073178). For the *Proechimys* analysis—for which we judged generic monophyly to be nonproblematic based on numerous previous analyses of echimyid relationships (but see Dalapicolla et al., 2024)—we used an exemplar sequence of *Hoplomys gymnurus* (KU892779) for rooting. GenBank accession numbers for the ingroup sequences we analyzed for this report are provided in appendices 3 and 4.

Ethnobiological Methods

Recorded monologs: From May to July of 1998 we elicited monologs about the natural history of local mammals from hunters at four Peruvian Matses villages, and we recorded these interviews on digital minidisk. All monologs were recorded in the Matses language. To elicit these texts, informants were asked to talk about a single mammalian folk taxon (e.g., kaksi [the pygmy squirrel]), which was mentioned only once by the interviewer (D.W.F.). Informants were asked to say as much as they liked about any topic relating to the taxon in question (see Voss and Fleck, 2017: appendix 1 for a free English translation of a recorded monolog about armadillos). Each informant's monologs were recorded with no other adults present to achieve independence of response. For each taxon, the interview was replicated a total of seven or eight times with different informants. These recordings were subsequently transcribed and translated by D.W.F. and literate Matses assistants. The texts were then checked with speakers other than the narrators to obtain second opinions on the validity of some of the less commonly asserted natural history details.

Sentences in the translated texts were sorted by topic (physical appearance, habitat preference, social behavior, vocalizations, daily activities, and food), and then combined to obtain composite essays for each taxon. These essays, which are presented under the heading "Matses natural history" in the accounts that follow, are supplemented by parenthetical editorial comments only as necessary to interpret otherwise obscure passages or to identify botanical taxa corresponding to Matses plant names. To provide a more complete ethnographic picture, topics concerning Matses nomenclature, classification, hunting strategies, and cultural significance—summarized under the heading "Ethnobiology" in each species account—were elaborated using data from additional sources, including interview-style question-and-answer sessions.

Plant identifications: Most of the plants mentioned by the Matses in their monologs were identified by various means. Palms were collected by D.W.F. in 1998 and 1999 from the area surrounding Nuevo San Juan with the help of Matses assistants, who named the palms while in the forest (before plant specimens were collected). Palm specimens were subsequently identified using published identification guides (Henderson, 1994; Henderson et al., 1995), and voucher material was deposited at the herbarium of the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (Lima) and in the New York Botanical Garden (New York). Other plants, particularly dicotyledonous trees, were identified by D.W.F. and two Matses assistants at the arboretum of the Instituto de Investigaciones de la Amazonía Peruana. This arboretum is maintained at the Centro de Investigaciones Jenaro Herrera, a forestry research station located about 80 km NW of Nuevo San Juan, where Swiss botanists had previously identified all trees >10 cm at breast height (Spichiger et al., 1989, 1990). Plants and trees in the proximity of Nuevo San Juan were also identified by D.W.F. using identification keys in Gentry (1993).

Botanical taxa corresponding to Matses plant names are provided using the following conventions: (1) Only the generic name is given if the Matses plant name corresponds to all the local species in a locally polytypic genus (e.g., bin,

which refers to all the local species of the genus *Castilla* [Moraceae]). (2) The generic name is followed by "sp." if the Matses plant name corresponds to just one unidentified local species in a genus (e.g., ichibin, which refers to an unidentified species of *Matisia* and another of *Eriotheca* [Bombacaceae]). (3) The generic name is followed by "spp." if the Matses plant name corresponds to two or more unidentified species, but not to all the local species of that genus (e.g., shankuin, which refers to multiple unidentified local species of *Pourouma* [Moraceae]). Where alternative technical names for plant families are current in the literature (e.g., Palmae vs. Arecaceae, Clusiaceae vs. Guttiferae), the nomenclature used here follows Gentry (1993).

SYSTEMATIC ACCOUNTS

The 40 rodent species herein reported from the Yavarí-Ucayali interfluve include one family of sciuromorphs (Sciuridae), one family of myomorphs (Cricetidae), and six families of caviomorphs (Caviidae, Cuniculidae, Dasyproctidae, Dinomyidae, Erethizontidae, and Echimyidae). In the accounts that follow we list the specimens we examined, explain our application of names to taxa, provide phenotypic and genetic data as necessary to support our taxonomic conclusions, and summarize Matses ethnomammalogical information as explained above. Under the heading "Remarks" we summarize information about the habitat(s) in which specimens were collected or observed, discuss agreements or discrepancies between Matses natural history accounts and the scientific literature, and comment on the probable trophic role of the species.

The taxonomic sequence in these accounts follows Patton et al. (2015) except as necessitated by new names and new binomial combinations.

Sciuridae

The taxonomy of Neotropical sciurids has long been disputed (Allen, 1915a; Moore, 1959; Vivo and Carmignotto, 2015; Abreu et al., 2020b), and

the resolution of several nomenclatural issues associated with the species treated below is beyond the scope of this study. Indeed, some of these problems are among the most frustrating that the first author has encountered in four decades of systematic research on mammals. The best we can do at this point is to document the basis for our binomial usage and explain why various alternatives seem less appropriate.

The five sciurid species that occur in our region include the pygmy squirrel (*Sciurillus pusillus*), which is often placed in its own tribe or subfamily in recognition of its wide phenotypic and genetic divergence from other squirrels (Mercer and Roth, 2003; Vivo and Carmignotto, 2015; Abreu et al., 2022). The remaining four species in our region belong to a monophyletic, predominantly Neotropical radiation of tree squirrels (Sciurinae: Sciurini) that has usually been partitioned among two or more genera based on morphological characters that are now known to be homoplastic (e.g., mammary counts and numbers of premolars; Abreu et al., 2020b). The most recent classification of Sciurini recognized 13 genera and one unnamed clade based on phylogenetic analyses of mtDNA sequence data (Abreu et al., 2020b), but it is not yet known whether any of these taxa are morphologically diagnosable, and the proposed restriction of *Sciurus* to just three Old World species would disrupt binomial usage for many New World species with previously undisputed names and a large ecological literature. The latter include *S. carolinensis* and *S. niger*, which would be known as *Neosciurus carolinensis* and *Parasciurus niger*, respectively, in Abreu et al.'s system.[1]

Instead, we treat all Abreu et al.'s (2020b) genera of Sciurini (except Asian *Reithrosciurus* and North American *Tamiasciurus*) as subgenera of *Sciurus*. This alternative classification is mono-

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[1] The names *Sciurus carolinensis* and *S. niger* have been used consistently for >200 years and occur in numerous publications on the North American fauna. The binomen *Sciurus carolinensis*, for example, appears in >12,000 articles indexed by Google Scholar (https://scholar.google.com; accessed 10 May 2021).

TABLE 1

Alternative Identifications for Species of Sciurini in the Yavarí-Ucayali Interfluve

This report	Abreu et al. (2020b)	Vivo and Carmignotto (2015)
Sciurus (*Hadrosciurus*) *pachecoi*	*Hadrosciurus* "species 3"	*Guerlinguetus aestuans* (part)
		Notosciurus pucheranii (part)
Sciurus (*Hadrosciurus*) *pyrrhinus*	*Hadrosciurus pyrrhinus*	*Hadrosciurus pyrrhinus*
Sciurus (*Hadrosciurus*) *spadiceus*	*Hadrosciurus spadiceus*	*Hadrosciurus spadiceus*
Sciurus ("*Microsciurus*") *flaviventer*	"*Microsciurus*" *flaviventer*	*Microsciurus flaviventer*

phyletic, and it only affects traditional binomial usage (Thorington and Hoffmann, 2005) for the handful of species formerly referred to *Syntheosciurus* and *Microsciurus*. Therefore, we use the following names in the accounts that follow: *Sciurus* (*Hadrosciurus*) *pyrrhinus* for the "southern red squirrel" of Vivo and Carmignotto (2015), *S.* (*H.*) *spadiceus* for the "northern red squirrel," *S.* (*H.*) *pachecoi* for a new species that could be called "Pacheco's squirrel," and *S.* ("*Microsciurus*") *flaviventer* for the "Amazon dwarf squirrel." Synonymous binomial usage for these taxa in recent publications is summarized in table 1.[2] For want of a better term, we refer collectively to the largest sciurines in our region (*S. pyrrhinus* and *S. spadiceus*) as "giant squirrels."

MEASUREMENTS: We measured the following dimensions of squirrel skulls and teeth (fig. 3):

CIL, condyloincisive length: from the greater curvature of one upper incisor to the articular surface of the occipital condyle on the same side.

LD, length of diastema: from the lesser curvature of an upper incisor to the crown of the anteriormost cheektooth (P3 or P4).

LIF, length of incisive foramen: greatest anterior-posterior dimension of either the left or right incisive foramen.

BIF, breadth of incisive foramina: greatest transverse dimension across both foramina.

MTR, maxillary toothrow: crown length of the cheektooth series (from P3 or P4 to M3).

BM1, breadth of M1: greatest transverse dimension of the crown of either the left or right first upper molar.

BPB, breadth of palatal bridge: breadth of the palate between the crowns of the right and left first upper molars.

LN, length of nasals: greatest anterior-posterior dimension of one nasal bone.

BR, breadth of rostrum: greatest transverse dimension of the rostrum, measured at the point where the maxillary-premaxillary suture intersects the lateral rostral margin on each side.

LIB, least interorbital breadth: the least transverse dimension between the orbits across the frontal bones.

ZB, zygomatic breadth: the greatest transverse dimension across the zygomatic arches.

OW, orbital width: the greatest width of either the left or right orbit, measured from the dorsal rim posterior to the supraorbital notch to the ventral margin (usually at or near the maxillary-jugal suture).

DI, depth of incisor: the perpendicular distance from the greater to the lesser curvature of one lower incisor.

SQUIRREL QUALITATIVE CHARACTERS: Some of the external and craniodental characters mentioned in the following accounts will be familiar to mammalogical readers, but several merit brief explanations.

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[2] We use "*Microsciurus*" (in scare quotes, following Abreu et al., 2020b) for the species formerly placed in *Microsciurus* that do not belong to the same clade as the type species, *Sciurus alfari* J.A. Allen, 1895. Unfortunately, no other genus-group name is based on any of these orphaned species, and the lineage to which they belong seems to lack diagnostic morphological traits.

FIG. 3. Dorsal, ventral, and lateral cranial views of *Sciurus spadiceus* illustrating the anatomical limits of sciurid craniodental measurements defined in the text.

TABLE 2

Selected Morphological Contrasts among Five Species of Squirrels from the Yavarí-Ucayali Interfluve
See text for explanations of morphological descriptors.

	Sciurillus pusillus	Sciurus pachecoi	Sciurus pyrrhinus	Sciurus spadiceus	Sciurus flaviventer
Head-and-body length	96–111 mm[a]	180–210 mm	268–278 mm	250–287 mm	139–145 mm
Hind foot length	27–28 mm[a]	49–56 mm	65–75 mm	65–73 mm	38–42 mm
Dorsal pelage	grizzled brownish	grizzled brownish	reddish	reddish or blackish	grizzled brownish
Postauricular patches	white	absent	orange	absent	pale buff or gray
Mammae	six	eight	eight	eight	six
Jugal-frontal contact	present	absent	absent	absent	absent
Sagittal crest[b]	absent	absent	absent	usually present	absent
AP versus SF contact[c]	SF	variable	AP	usually AP	SF
Accessory oval foramen	absent	usually present	usually present	usually present	usually absent
SPF & DPF[d]	separate	separate	separate	usually confluent	separate
Sphenopalatine vacuities[e]	small	variable	very small or absent	consistently large	very small or absent
Upper incisors[f]	procumbent	not procumbent	not procumbent	not procumbent	procumbent
Upper premolars[g]	two	one	one	one	two

[a] Measurements of subadults; adult dimensions are probably a few millimeters longer.
[b] On interparietal bone.
[c] AP = alisphenoid-parietal; SF = squamosal-frontal.
[d] SPF = sphenopalatine foramen; DPF = dorsal palatine foramen.
[e] In roof of mesopterygoid fossa.
[f] Procumbent = proodont sensu Thomas (1919); not procumbent = orthodont or opisthodont sensu Thomas (1919).
[g] Number in each maxillary cheektooth row.

1. Postauricular patches are small regions of pale, self-colored (not grizzled or gray-based) fur that occur behind (medial to) the pinnae and contrast with the surrounding darker fur of the head. Although seemingly insignificant features, postauricular patches are consistently present in some species but indistinct or absent in others (fig. 4, table 2). The presence or absence of postauricular patches can be hard to determine on skins with dried pinnae that are closely applied to the head, but gentle pressure on the pinna is often sufficient to reveal the postauricular fur.

2. Mammary counts tend to be highly constant among conspecific females of Neotropical squirrels (Allen, 1915a; Moore, 1961). Following Moore (1961) we only counted mammae from obviously parous specimens in which the entire mammary row was exposed on both sides of the abdomen (inguinal mammae are sometimes concealed in folds of carelessly prepared skins). Among the species in our region and others that we compared with them, either six or eight mammae were consistently observed, with just one case of intraspecific polymorphism.[3]

3. Patterns of contact among the bones comprising the lateral braincase vary among species of Neotropical squirrels. Whereas some species—for example, Sciurus (Guerlinguetus) aestuans and Sciurus (Leptosciurus) pucheranii—always or usually exhibit contact between the squamosal and frontal bones (fig. 5A), other species (especially in the subgenus Hadrosciurus) often exhibit contact between the alisphenoid and the parietal (fig. 5B). This character (squamosal-frontal versus alisphe-

[3] A single fluid-preserved specimen of Sciurus spadiceus (AMNH 272860) has seven mammae.
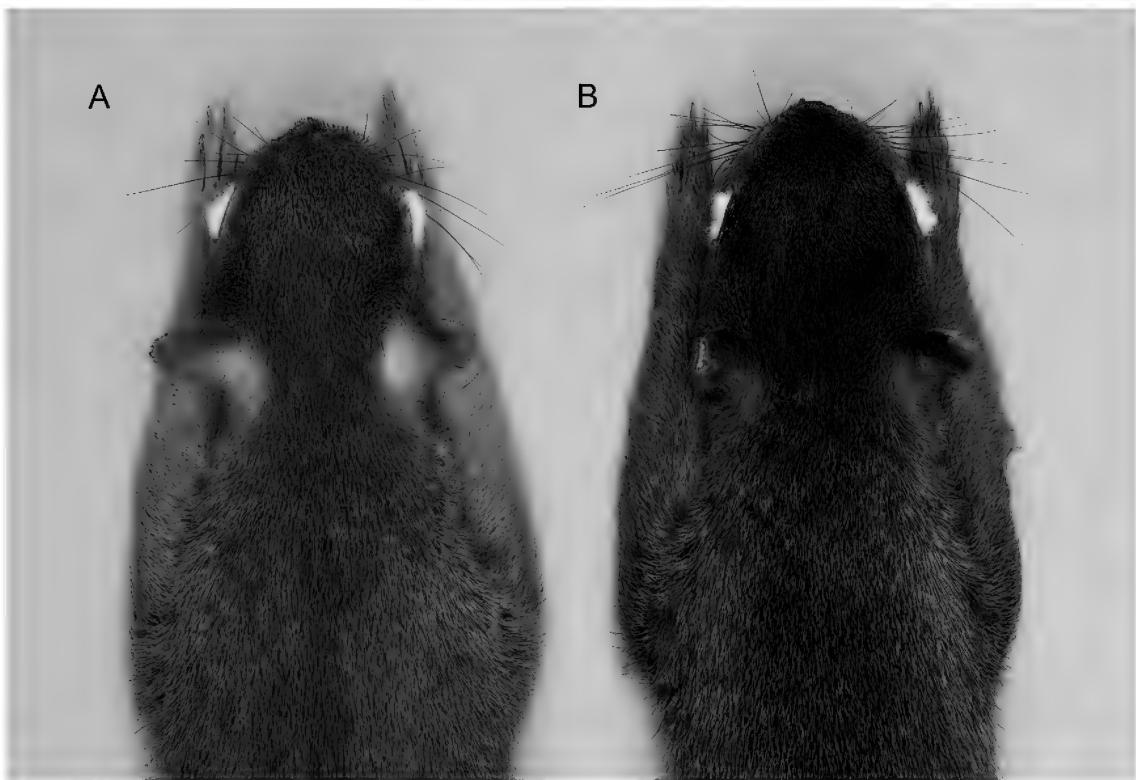
FIG. 4. Dorsal views of the forelimbs and head of *Sciurus pyrrhinus* (**A**, AMNH 73874) and a red-phase specimen of *S. spadiceus* (**B**, AMNH 73870). Whereas postauricular patches are always conspicuous in *S. pyrrhinus*, they are inconspicuous or absent in *S. spadiceus*. Head coloration (grizzled reddish in *S. pyrrhinus*, blackish in *S. spadiceus*) and forelimb coloration (clear orange in *S. phyrrhinus*, grizzled reddish in *S. spadiceus*) are other distinguishing external characters.

noid-parietal contact) is familiar to marsupial taxonomists, who often score it for phylogenetic analysis, but it seems not to have been used previously in rodent systematics. Nevertheless, it usefully distinguishes some of the taxa in our interfluvial region and elsewhere (table 2).

4. Sphenopalatine vacuities are paired lateral openings in the roof of the mesopterygoid fossa of many rodents (e.g., cricetids; Voss, 1993: fig. 7). When present in Neotropical squirrels, these openings usually flank the basisphenoid-presphenoid suture. They are consistently large and well developed in some species (e.g., *Sciurus spadiceus*) but are just as consistently indistinct or absent in others (e.g., *S. pyrrhinus*). In yet other species (e.g., *S. pachecoi*) they are variably present or absent.

5. The foramen ovale is a large, undivided, ventrally directed opening in the alisphenoid just anterior to the auditory bulla on each side of the skull in some squirrels (fig. 6A), but in others the foramen ovale is divided by a bridge of bone (fig. 6B). Of the two openings thus formed, the lateral orifice is known as the accessory foramen ovale (foramen ovale accessorius; Wahlert, 1974) or accessory oval foramen. Despite some intraspecific polymorphism, this feature is sometimes useful for distinguishing taxa (e.g., *Sciurus pachecoi* from *S. ignitus*; see below).

6. The foramina that perforate the medial wall of the orbit exhibit noteworthy taxonomic variation in Neotropical squirrels. In most species the sphenopalatine and dorsal palatine foramina are separate openings (fig. 7A), but
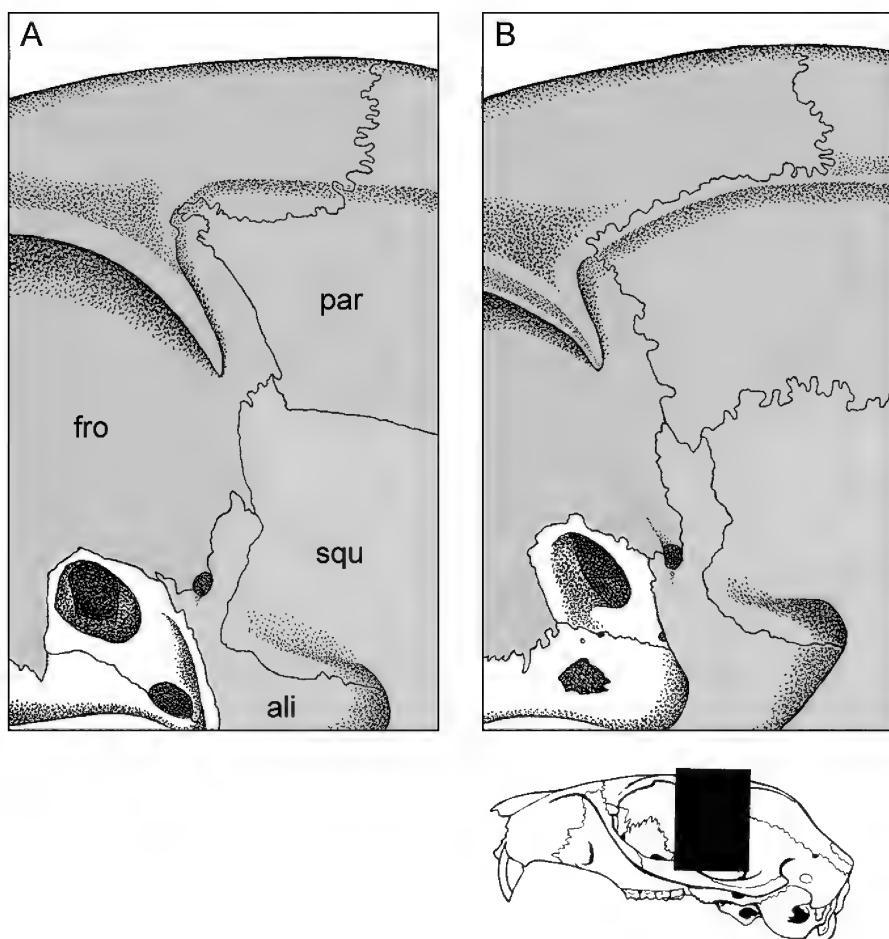
FIG. 5. Alternative patterns of bony contact on the lateral braincase of *Sciurus aestuans* (**A**, AMNH 267013; with squamosal-frontal contact) and *S. pachecoi* (**B**, AMNH 73921; with alisphenoid-parietal contact). Abbreviations: **ali**, alisphenoid; **fro**, frontal; **par**, parietal; **squ**, squamosal.

the sphenopalatine foramen[4] is sometimes so large that the dorsal palatine foramen opens within it (fig. 7B). When these foramina are confluent, the sphenopalatine foramen is usually larger than the adjacent optic foramen, but when they are separate the sphenopalatine foramen can be the same size, smaller, or larger than the optic foramen.

7. The scars on the dorsolateral braincase that mark the origin of the temporalis muscle converge posteriorly in *Sciurus spadiceus* to form a distinct sagittal crest along the midline of the interparietal bone in almost all examined specimens of that species (fig. 8A). The temporalis scars converge posteriorly over the interparietal in *S. pyrrhinus* too, but they remain separated by a millimeter or more and do not form a distinct midline crest (fig. 8B). The temporalis scars of other squirrels in our region are only weakly convergent and remain widely separated as they approach the occiput (fig. 8C–D).

SQUIRREL AGE CRITERIA: As defined herein, adult squirrels have completely erupted maxil-

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[4] Hershkovitz (1959: 346) called this opening the sphenopalatine "fissure." Our usage follows Wahlert (1974).
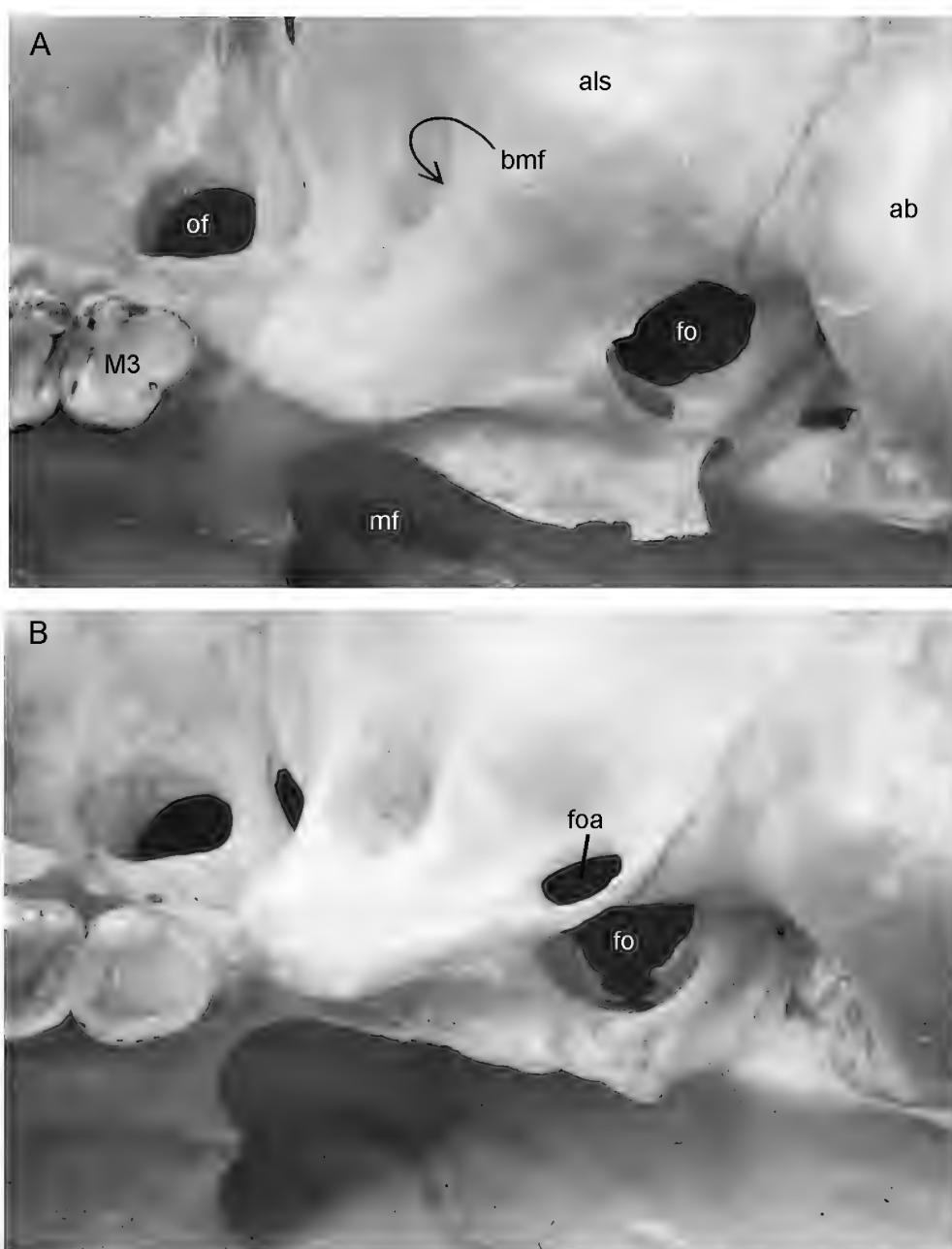
FIG. 6. Left ventrolateral cranial views of *Sciurus ignitus* (**A**, AMNH 246663) and *S. pachecoi* (**B**, AMNH 73921). Abbreviations: **ab**, auditory bulla; **als**, alisphenoid; **bmf**, buccinator-masticatory foramen; **fo**, foramen ovale; **foa**, foramen ovale accessorius; **M3**, third upper molar; **mf**, mesopterygoid fossa; **of**, optic foramen.
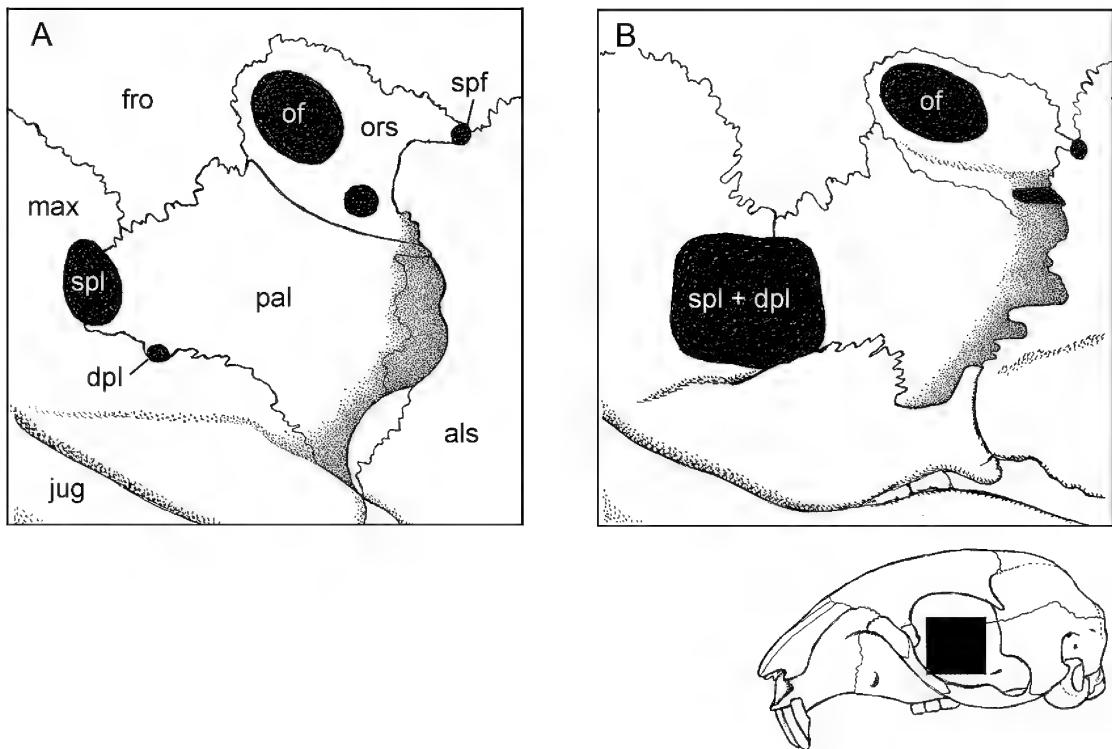
FIG. 7. Anterodorsolateral view of the orbit in *Sciurus pyrrhinus* (**A**, AMNH 73864) and *S. spadiceus* (**B**, AMNH 272860) illustrating species differences in foraminal size and configuration. Abbreviations: **als**, alisphenoid; **dpl**, dorsal palatine foramen; **fro**, frontal; **jug**, jugal; **max**, maxillary; **of**, optic foramen; **ors**, orbitosphenoid; **pal**, palatine; **spf**, sphenofrontal foramen; **spl**, sphenopalatine foramen.

lary toothrows (P3–M3 or P4–M3 depending on species; see below) and they exhibit characteristic patterns of fusion among cranial bones. Mature skulls of *Sciurillus* have completely fused dorsal braincase elements (e.g., lacking the frontoparietal suture; Moore, 1959), but the basicranial sutures remain open. By contrast, mature sciurines (e.g., *Sciurus* spp.) retain the frontoparietal suture but exhibit fusion between the basioccipital and basisphenoid.

ETHNOBIOLOGY: The general term for squirrels in Matses is kapa, which is not linguistically analyzable, has no other meaning, and is the universal term for squirrels in other Panoan languages. Five named types of squirrels are recognized by the Matses, although Matses names are imperfectly correlated with biological taxa (see below).

Sciurillus pusillus (E. Geoffroy, 1803)

Figures 8E, 9

VOUCHER MATERIAL (*N* = 10): Nuevo San Juan (AMNH 268254, 272807, 272866; MUSM 11197, 13351, 13352), Santa Cecilia (FMNH 87182–87185).

UNVOUCHERED OBSERVATIONS: Estación Biológica Quebrada Blanco (Heymann and Knogge, 1997; Amasifuén and Heymann, 2017), Jenaro Herrera (Ríos et al., 1974; Tovar, 2011), San Pedro (Valqui, 1999, 2001), Tamshiyacu-Tahuayo Reserve (Jessen et al., 2013a; Palmer and Koprowski, 2015).
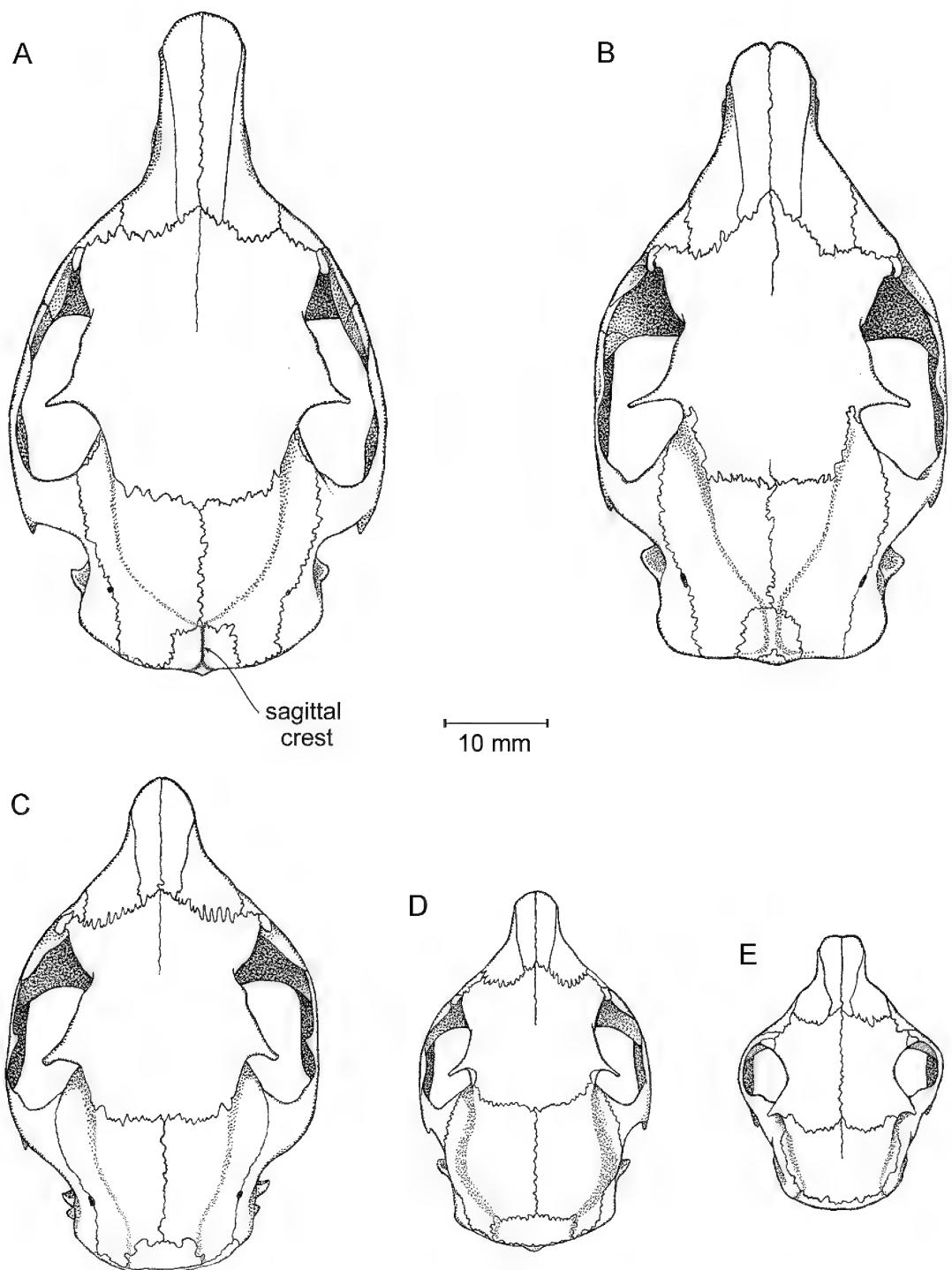
FIG. 8. Dorsal cranial views illustrating size and other diagnostic features of five sympatric species of squirrels from the Yavarí-Ucayali interfluve: *Sciurus spadiceus* (**A**, AMNH 268253), *S. pyrrhinus* (**B**, MUSM 13354), *S. pachecoi* (**C**, AMNH 73917), *S. flaviventer* (**D**, AMNH 268250), and *Sciurillus pusillus* (**E**, AMNH 272807).

TABLE 3

External and Craniodental Measurements (mm) of Four Subadult *Sciurillus pusillus*
from the Yavarí-Ucayali Interfluve

	Nuevo San Juan		Santa Cecilia	
	AMNH 272807	MUSM 13352	FMNH 87182	FMNH 87185
Sex	male	female	male	male
HBL	105	102	111	108
LT	111	102	95	—
HF	28	28	27	28
Ear	14	14	11	11
CIL	25.1	23.9	25.0	25.3
LD	6.3	5.6	5.8	5.8
LIF	2.3	2.2	2.6	2.1
BIF	1.2	1.2	1.3	1.1
MTR	4.4	4.7	4.7	4.7
BM1	1.1	1.3	1.4	1.3
BPB	4.1	4.2	3.8	3.7
LN	7.7	7.6	8.2	8.4
LIB	12.0	11.8	12.5	12.6
ZB	18.7	19.0	19.2	19.3
OW	6.7	6.6	6.6	6.7
DI	1.5	1.4	1.5	1.5

IDENTIFICATION: The pygmy squirrel is much smaller than the other four sciurid species in our region (fig. 8, tables 2, 3),[5] from which it also differs in numerous qualitative characters. The latter include those listed in table 2 together with others reported by Moore (1959) and Vivo and Carmignotto (2015). Our material conforms to the description of western Amazonian specimens of *Sciurillus pusillus* provided by Anthony and Tate (1935), and we acknowledge the deep genetic divergence between sequenced specimens from French Guiana—the type locality— and Peru (Mercer and Roth, 2003), but we agree with Vivo and Carmignotto (2015) that the material at hand is insufficient to diagnose addi-

tional species of pygmy squirrels. Unfortunately, if a name were needed for any western Amazonian form, the application of *kuhlii* Gray, 1867, will need to be resolved in some fashion. The type locality for this problematic name is "Brazil," and Thomas's (1928) "restriction" of the type locality to Pebas (on the north bank of the Amazon in Loreto department, Peru) was not based on any certain knowledge of where the type was actually collected.

ETHNOBIOLOGY: The Matses name for the pygmy squirrel is kaksi, a term that is not linguistically analyzable, but may be of onomatopoetic origin. It is classified by the Matses as a type of kapa ("squirrel"). The Matses do not recognize any subtypes and have no synonymous names for this species.

The pygmy squirrel is not eaten, killed, or considered a pest. The Matses see them fre-

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[5] The only available weight data from our region were obtained from subadults, four of which weighed 31–35 g. According to Vivo and Carmignotto (2015), the average weight of this species is 44 g.

FIG. 9. Dorsal, ventral, and lateral cranial views of *Sciurillus pusillus* (AMNH 272807, a subadult specimen). The lateral view of the skull is a reversed image of the right side because the left side is damaged. All views about ×2.0.

quently when they are in the forest. It is considered a very good pet, though they sometimes run off when they become adults. The Matses say that pet pygmy squirrels eat people's lice.

MATSES NATURAL HISTORY: The pygmy squirrel is tiny and grayish. It has whiskers on its snout, white patches on its ears, and a somewhat bushy tail. The skin of its tail slips off easily when grabbed. The male has impressively large testicles.

The pygmy squirrel is strictly arboreal. They are found in all habitats, including secondary forest.

The pygmy squirrel makes its nest in a termite nest (i.e., by excavating a chamber in a termite nest) halfway up the trunk of a tree. It lines the inside with strips of the shredded bark of tote trees (*Eschweilera* spp., *Lecythis* spp., or *Cariniana* [Lecythidaceae]).

The pygmy squirrel is diurnal and spends most of the day on the trunks of large trees, gnawing on
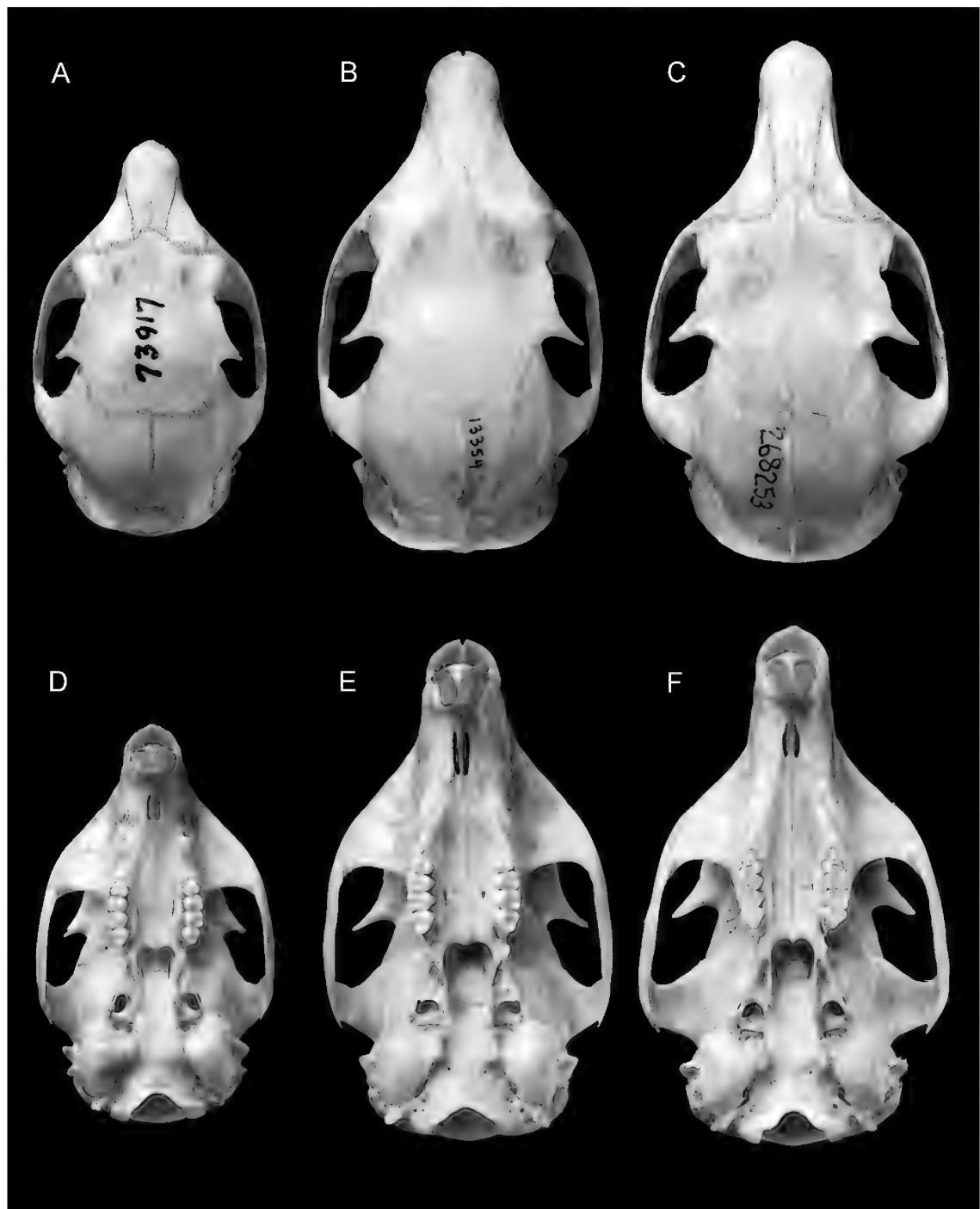
FIG. 10. Dorsal and ventral cranial views of *Sciurus pachecoi* (**A**, **D**, AMNH 73917), *S. pyrrhinus* (**B**, **E**, MUSM 13354), and *S. spadiceus* (**C**, **F**, AMNH 268253). All views about ×1.2.
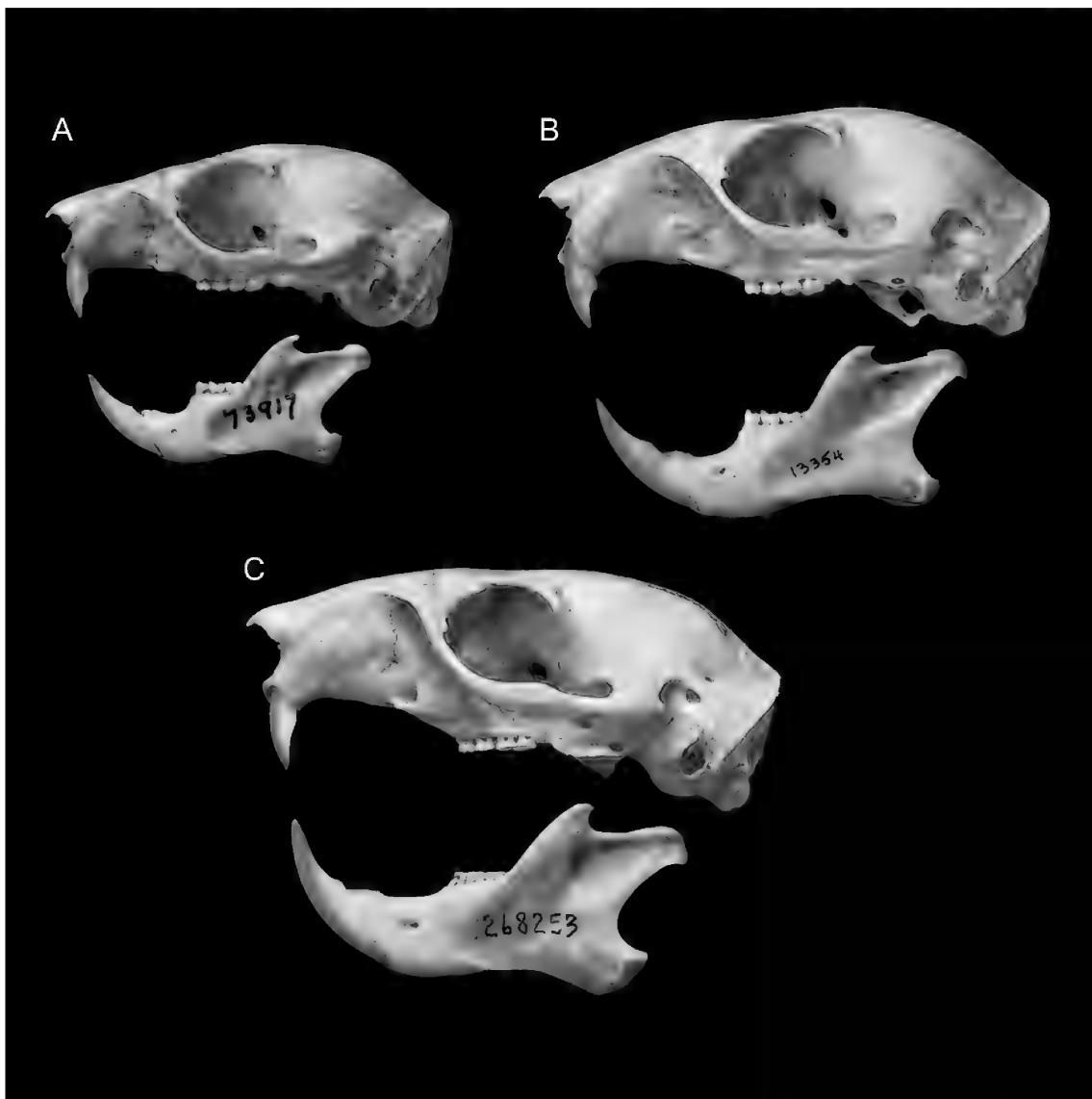
FIG. 11. Lateral cranial views of *Sciurus pachecoi* (**A**, AMNH 73917), *S. pyrrhinus* (**B**, MUSM 13354), and *S. spadiceus* (**C**, AMNH 268253). All views about ×1.1.

the bark. It always returns to the same trees. It always gnaws on the same trees, returning to the same trees regularly. As it descends a tree, it keeps its tail against the tree trunk. It hides on the opposite side of the tree when it sees people.

Pygmy squirrels are often found in small groups of two or three.

Margays and snakes prey on pygmy squirrels. Pygmy squirrels bite people when they are grabbed.

The pygmy squirrel calls with a high-pitched "pisss pisss pisss." It also chatters "cha cha cha cha cha."

The pygmy squirrel eats the bark of the trunks and branches of trees with smooth bark, especially one type of tree called kaksin dapete, "one that the pygmy squirrel eats" (*Macrolobium* spp. [Leguminosae/Caesalpinioideae] or *Pithecellobium* [Leguminoseae/Papilionoideae]).

TABLE 4

Specimens of *Sciurus pachecoi* and *S. ignitus* Collected by the Olallas Near Sarayacu on the Río Ucayali in 1927

AMNH #	Species	Date	Camp[a]	Side of river[a]
76442	*ignitus*	16 March	1	right ("east")
76443	*pachecoi*	28 March	1	right ("east")
76326	*ignitus*	6 April	1	right ("east")
76325	*ignitus*	15 April	1	right ("east")
76444	*ignitus*	15 April	1	right ("east")
76467	*ignitus*	1 May	1	unknown
76466	*ignitus*	10 June	2	left ("west")
75278	*pachecoi*	4 August	3	right ("east")
75277	*pachecoi*	10 August	3	right ("east")

[a] According to Wiley's (2010: 41–43) narrative of the Olallas' Peruvian fieldwork. Cardinal directions in scare quotes indicate macrogeographic orientations; due to river meanders, local compass directions might differ (e.g., right-bank localities could be north, south, east, or west of left-bank localities).

REMARKS: All our specimens from Nuevo San Juan were shot by Matses hunters in the daytime from trees in primary forest. Four specimens were collected in well-drained (terra firme) forest, one was in flooded forest, and another was in riverside forest of unknown character. One specimen was described as having been shot while feeding on the surface of bark while clinging to the underside of a branch about 35 m above the ground.

Matses observations about the natural history of pygmy squirrels are consistent with the modest literature on this topic, notably including their habitual association with particular large trees, their habit of feeding on bark—or, more plausibly, on something that is found on the surface of bark (possibly exudates)—and their excavation of arboreal termitaria as nests (Heymann and Knogge, 1997; Jessen et al., 2013a; Palmer and Koprowski, 2015).

Sciurus (*Hadrosciurus*) *pachecoi*, new species

Figures 5B, 6B, 8C, 10A, 10D, 11A, 13, 15

Hadrosciurus "species 3": Abreu et al., 2020b: 8 (informal name for an undescribed putative species identified by phylogenetic analysis of mtDNA sequence data).

HOLOTYPE: AMNH 73924, consisting of the skin and skull of an adult female collected at Orosa (on the right bank of the Amazon at or near the mouth of the Río Orosa; see appendix 1), Loreto department, Peru, by Alfonso and Ramón Olalla on 21 September 1926. The tip of the tail is missing, but the specimen is otherwise intact. A complete mitochondrial genome from this specimen was analyzed by Abreu et al. (2020b), who deposited the sequence in GenBank with accession number OM154952.

OTHER VOUCHER MATERIAL (*N* = 25): Nuevo San Juan (AMNH 268251, MUSM 13353), Orosa (AMNH 73917–73923, 754079–74083), Quebrada Esperanza (FMNH 88982, 88983), Quebrada Vainilla (LSUMZ 28416, 28417), San Fernando (FMNH 88981), Santa Cecilia (FMNH 87173–87177).

OTHER SPECIMENS EXAMINED: In addition to the 26 specimens from the Yavarí-Ucayali interfluve listed above, we examined three others (AMNH 76443, 75277, 75278) collected just outside our region on the right ("east") bank of the lower Ucayali. Although these specimens are all labelled "Sarayacu," documentary evidence summarized by Wiley (2010: 41–43) suggests that they came from two different camps (table 4), one opposite the town of Sarayacu (ca.
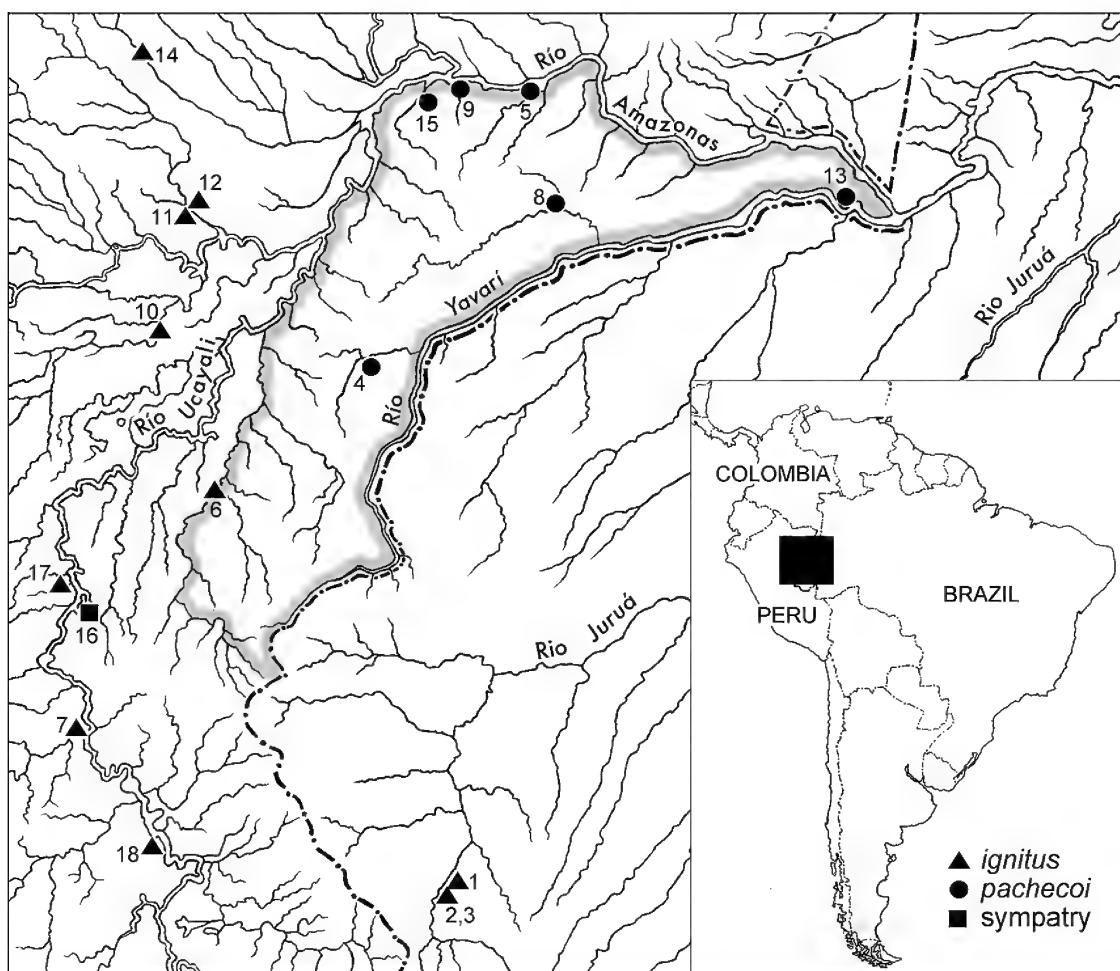
FIG. 12. Collection localities of *Sciurus pachecoi* and *S. ignitus* in northeastern Peru and western Brazil. (The boundaries of the Yavarí-Ucayali interfluve are shaded.) Key to localities: **1**, Brazil, Acre, Nova Vida on Rio Juruá; **2**, Brazil, Acre, Ocidente on Rio Juruá; **3**, Brazil, Acre, Igarapé Porongaba on Rio Juruá; **4**, Peru, Loreto, Nuevo San Juan on Río Gálvez; **5**, Peru, Loreto, Orosa on Río Amazonas; **6**, Peru, Loreto, Puerto Punga on Río Tapiche; **7**, Peru, Loreto, "Pisqui River" [mapped at confluence with Río Ucayali]; **8**, Peru, Loreto, Quebrada Esperanza on Río Yavarí Mirím; **9**, Peru, Loreto, Quebrada Vainilla [at confluence with Río Amazonas]; **10**, Peru, Loreto, Río Samiria [at Estación Pithecia]; **11**, Peru, Loreto, Río Tigre; **12**, Peru, Loreto, Río Tigrillo [1 km above mouth, on Río Tigre]; **13**, Peru, Loreto, San Fernando on Río Yavarí; **14**, Peru, Loreto, Santa Luisa on Río Nanay; **15**, Peru, Loreto, Santa Cecilia on Río Manití; **16**, Peru, Loreto, Sarayacu [Camps 1 and 3] on Río Ucayali; **17**, Peru, Loreto, Sarayacu [Camp 2] on Río Ucayali; **18**, Peru, Ucayali, Yarinacocha on Río Ucayali.
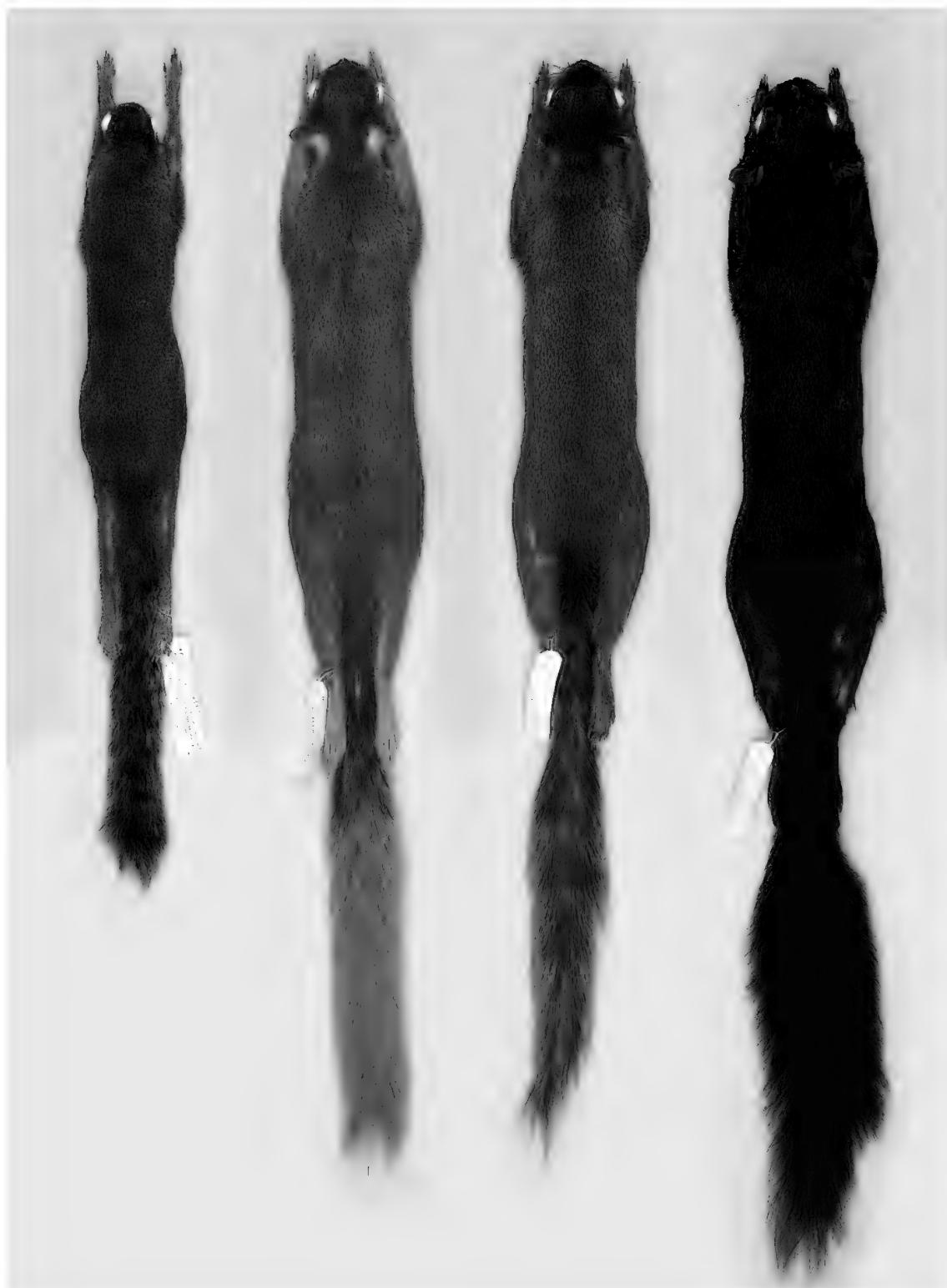
6°47′S, 75°07′W) and the other a few kilometers upriver near the modern town of Orellana (ca. 6°55′S, 75°09′W).

OTHER INTERFLUVIAL RECORDS:[6] Actiamë (Amanzo, 2006), Anguila (Escobedo-Torres, 2015), Itia Tëbu (Amanzo, 2006), Río Yavarí-Mirím (Salovaara et al., 2003), San Pedro (Valqui, 1999, 2001).

DISTRIBUTION AND SYMPATRY: *Sciurus pachecoi* is only known from the Peruvian department of Loreto, where it has been collected south of the Amazon and east of the Ucayali (fig. 12). In the Yavari-Ucayali interfluve (e.g., at Nuevo San Juan) it occurs sympatrically with *Sciurillus pusillus*, *S. pyrrhinus*, *S. spadiceus*, and *S. flaviventer*. On the right ("east") bank of the Ucayali opposite Sarayacu it additionally occurs with *S. ignitus*, which it closely resembles in size and dorsal coloration (see below).

DESCRIPTION: This is a medium-sized (230–280 g) squirrel that is uniformly grizzled brownish dorsally from nose to rump (fig. 13), without any markings other than a narrow ring of pale-orange fur around each eye. Postauricular patches of contrastingly pale fur behind the pinnae are absent. The tail is lightly frosted with orange, but it is not banded or otherwise patterned. The ventral pelage is abruptly paler from chin to anus, including the insides of the fore- and hind limbs. The predominant ventral coloration is yellowish orange, paler in some individuals than in others, but at least some of the ventral hairs (especially posteriorly) have grayish bases. All adult female specimens with countable mammae ($N = 4$) have eight teats.

The skull (fig. 10A, 10D, 11A) is unremarkable in gross morphology (resembling those of many other squirrels of similar size), without unusual rostral, zygomatic, or bullar proportions. The sphenopalatine foramen (in the

anteromedial wall of the orbit) and the dorsal palatine foramen (in the floor of the orbit) are always separate, but the sphenopalatine vacuities (in the roof of the mesopterygoid fossa) are highly variable: small or even absent in some individuals (e.g., MUSM 13353) but quite large in others (e.g., AMNH 73917). The optic foramen is usually larger than the sphenopalatine foramen, and an accessory foramen ovale is almost always bilaterally present (fig. 6B). Of 18 adult specimens that could be scored for contacts among the alisphenoid, frontal, parietal, and squamosal bones on the lateral surface of the braincase, 12 exhibit alisphenoid-parietal contact, whereas 6 exhibit squamosal-frontal contact. The upper incisors are opisthodont or orthodont, and there is only a single premolar in each upper cheektooth row (P3 is absent).

COMPARISONS: *Sciurus pachecoi* differs conspicuously from three other members of the subgenus *Hadrosciurus*—*S. igniventris*, *S. pyrrhinus*, and *S. spadiceus*—which are all much larger and have reddish or blackish dorsal pelage (for additional contrasting traits of sympatric *S. pyrrhinus* and *S. spadiceus*, see table 2). Instead, *S. pachecoi* closely resembles *S. ignitus*, another species of the *Hadrosciurus* clade (sensu Abreu et al., 2020b).[7] *Sciurus pachecoi* and *S. ignitus* are mostly allopatric, but these species occur together on the right ("east") bank of the Ucayali just west of our region (table 4, fig. 12).

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[6] All originally reported as *Sciurus ignitus*.

[7] Abreu et al.'s (2020b) sequencing results and our examination of relevant type material (see below) are consistent with Vivo and Carmignotto's (2015: 41) hypothesis that the following nominal taxa are conspecific: *ignitus* Gray, 1867; *irroratus* Gray, 1867; *cuscinus* Thomas, 1902; *ochrescens* Thomas, 1914; *iquiriensis* Vieira, 1952; *boliviensis* Osgood, 1921; *argentinius* Thomas, 1921; and *sanborni* Osgood, 1944. However, we have not examined type material of *cabrerai* Moojen, 1958, which might or might not also be a synonym of *S. ignitus*. By contrast, neither Abreu et al.'s (2020b) results nor our examination of representative specimens supports Vivo and Carmignotto's (2015) hypothesis that any of these taxa are closely related to the species they called *Notosciurus pucheranii* (Fitzinger, 1867).

FIG. 13. Dorsal view of skins of squirrels in the subgenus *Hadrosciurus*. Left to right: *Sciurus pachecoi* (LSUMZ 28417), *S. pyrrhinus* (AMNH 73874), a red-phase specimen of *S. spadiceus* (AMNH 73870), and a black-phase specimen of *S. spadiceus* (AMNH 73881).
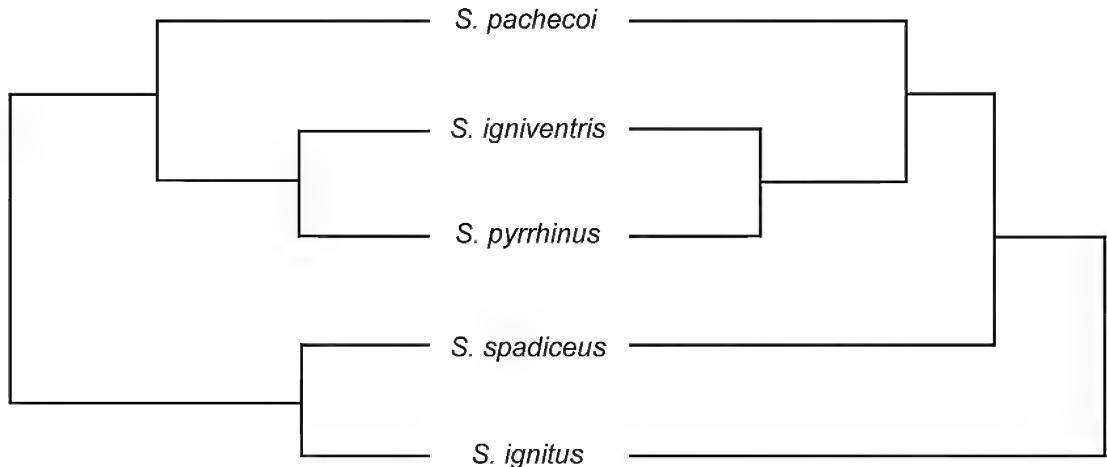
FIG. 14. Phylogenetic relationships of five species of *Sciurus* (subgenus *Hadrosciurus*) as recovered by maximum-likelihood analyses of mitogenomic sequence data (left, abstracted from Abreu et al., 2020b: fig. 4) and from 3841 UCE loci (right, abstracted from Abreu et al., 2022: fig. 7). All illustrated nodes in these diagrams received 100% bootstrap support; branch lengths are arbitrary. Only three of these species (*Sciurus pachecoi*, *S. pyrrhinus*, and *S. spadiceus*) are known to occur in the Yavarí-Ucayali interfluve.

Despite their external similarity, *S. pachecoi* and *S. ignitus* are not sister taxa, because each is more closely related to one or more of the larger reddish or blackish species of the *Hadrosciurus* group (fig. 14).

Like the present species, *Sciurus ignitus* is a medium-sized, albeit somewhat smaller (ca. 170–240 g) squirrel, with similarly unpatterned, uniformly grizzled-brownish or -olivaceous dorsal fur. However, all the specimens of *S. ignitus* that we examined have pale (usually orange, but sometimes yellowish or even whitish) postauricular patches. The ventral pelage of *S. ignitus* is highly variable across the species' considerable geographic range, but in the Peruvian department of Loreto, *S. ignitus* has much darker ventral fur than *S. pachecoi*, especially laterally and on the insides of the fore- and hind limbs (fig. 15). Lastly, parous adult females of *ignitus* with countable mammae ($N = 26$) invariably have just six teats.

Sciurus ignitus is very similar to *S. pachecoi* in cranial morphology but averages slightly smaller in most measured dimensions (table 5). Additionally, the sphenopalatine foramen of *S. ignitus* is usually equal to or larger than the optic foramen, the foramen ovale accessorius is almost always bilaterally absent (fig. 6A), and the alisphenoid and parietal are almost always in contact on the lateral braincase. Although few of these cranial differences are absolute (table 6), specimens with atypical traits for one character are not atypical in other respects, such that polymorphisms are seldom a problem for specimen identification.

One specimen of *Sciurus pachecoi* from the Yavarí-Ucayali interfluvium (AMNH 73917) was identified as *Guerlinguetus aestuans* by Vivo and Carmignotto (2015), who identified two others (FMNH 87173, 88981) as *Notosciurus pucheranii*. Neither identification is plausible in the context of Abreu et al.'s (2020b) phylogenetic results, but such discrepancies illustrate the still confused taxonomy of Neotropical squirrels and the urgent need for revisionary studies to reconcile molecular results with morphological character variation.

ETYMOLOGY: For Victor Pacheco, curator of mammals at the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, whose career accomplishments have substantially transformed Peruvian mammalogy and

TABLE 5

External and Craniodental Measurements (mm) of *Sciurus pachecoi* and *S. ignitus*

	S. pachecoi[a]	*S. ignitus*[b]
HBL	201 ± 8 (180–210) 11	190 ± 10 (165–205) 16
LT	188 ± 19 (153–214) 11	180 ± 16 (152–203) 16
HF	53 ± 2 (49–56) 22	48 ± 2 (45–51) 21
Ear	23 ± 1 (21–25) 11	22 ± 2 (19–26) 14
CIL	44.1 ± 0.7 (42.3–45.2) 19	41.7 ± 1.1 (39.6–43.6) 22
LD	13.2 ± 0.5 (12.1–14.1) 22	12.6 ± 0.5 (11.8–13.6) 21
LIF	3.3 ± 0.3 (2.8–4.0) 21	3.2 ± 0.3 (2.5–3.7) 24
BIF	1.9 ± 0.2 (1.4–2.2) 21	1.8 ± 0.2 (1.5–2.2) 24
MTR	7.8 ± 0.2 (7.3–8.1) 19	7.4 ± 0.4 (6.8–8.2) 23
BM1	2.2 ± 0.1 (2.0–2.6) 22	2.2 ± 0.1 (2.0–2.4) 23
BPB	6.6 ± 0.3 (6.1–7.1) 21	6.1 ± 0.4 (5.2–6.8) 22
LN	14.1 ± 0.6 (13.3–15.1) 20	13.2 ± 0.9 (11.1–14.7) 23
BR	12.2 ± 0.7 (10.6–13.2) 21	11.5 ± 0.6 (10.4–12.9) 25
LIB	16.2 ± 0.8 (14.5–17.4) 20	15.0 ± 0.6 (14.0–16.7) 24
ZB	29.3 ± 0.9 (27.4–30.6) 12	27.6 ± 1.0 (25.7–29.4) 18
OW	11.7 ± 0.3 (11.1–12.2) 17	10.8 ± 0.3 (9.9–11.6) 25
DI	3.3 ± 0.1 (2.9–3.5) 22	2.9 ± 0.2 (2.6–3.2) 25

[a] The mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size for measurements of the following series: AMNH 73917–73919, 73921–73924, 74079–74081, 268251; FMNH 88981–88983, 87173–87177; LSUMZ 28416, 28417; MUSM 13353.

[b] The mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size for measurements of the following series: AMNH 15803, 16560, 16562, 36490, 37189, 37190, 38765, 38766, 119401, 119402, 119404, 149145, 246662, 246663; FMNH 98060–98063, 98065; KU 144564, 144565; MSB 239309; MVZ 190349–190351.

established Lima as one of the most important centers of mammalian taxonomic research in South America.

ETHNOBIOLOGY: The Matses name for Pacheco's squirrel is kapampi ("little squirrel"). The Matses do not recognize any subtypes and have no synonymous names for this species. Pacheco's squirrel is not eaten by the Matses. It is occasionally kept as a pet.

MATSES NATURAL HISTORY: Pacheco's squirrel is yellowish. It is smaller and has a shorter tail than giant squirrels, but it is larger than pygmy squirrels.

Pacheco's squirrel is found in all habitats. They are encountered less frequently than giant squirrels.

Pacheco's squirrel makes its nest in hollowed-out termite nests that are attached to the sides of trees. It also makes nests in crevices of the deeply fluted trunks of iwi chuda trees (*Aspidosperma* spp., [Apocynaceae]) and in the crowns of pinchuk palms (*Astrocaryum murumuru*). It scrapes soft tree bark into strips to line its nest.

Pacheco's squirrel is mostly arboreal, walking on branches and climbing up vines. It comes down to the ground to pick up fallen fruits, but it carries them back up to a tree branch to eat them. It gathers fruits or palm nuts into piles before taking them up to eat one by one.

Pacheco's squirrel is found alone or in pairs.

Hawks prey on Pacheco's squirrel.

TABLE 6

Qualitative Morphological Comparisons between *Sciurus pachecoi* and *S. ignitus*

	S. pachecoi	*S. ignitus*
Ventral pelage	pale yellow-orange	dark orange[a]
Postauricular patches	absent	present
Mammae	eight	six
Sphenopalatine foramen	usually < optic foramen	usually ≥ optic foramen
Accessory oval foramen	usually present	usually absent

[a] In northeastern Peru (ventral coloration is geographically variable; see text).

Pacheco's squirrel eats the endosperm of ripe <u>pinchuk</u> palm (*Astrocaryum murumuru*) nuts. It eats the pulp and/or seeds of dicot tree fruits, including <u>kuëte mëdiad</u> trees (an unidentified tree with starchy fruits that the Matses cook before eating) and <u>tonnad</u> trees (Myristicaceae spp.).

REMARKS: Matses observations provide the only available information about the behavior and diet of this species. One of our specimens from Nuevo San Juan (AMNH 268251) was shot as it perched on a branch in the canopy of primary upland forest beside a small stream in the late morning. The other (MUSM 13353) was also shot in primary upland forest, but no other ecological information was recorded about it. Both specimens from the Quebrada Vainilla were also shot in upland forest (S. Cardiff, personal commun.), but the large series from Orosa was collected in the floodplain of the Amazon, probably in *várzea* (Wiley, 2010: 40). Although more ecological data would be welcome, these observations suggest *Sciurus pachecoi* is not a habitat specialist.

SPECIMENS OF *SCIURUS IGNITUS* EXAMINED (*N* = 80): **Bolivia**—No other locality data (BMNH 46.7.28.27 [holotype of *ignitus*]); *Cochabamba*, Alto Palmar (AMNH 119401, 119402), Incachaca (AMNH 38765), San Mateo (AMNH 119404); *La Paz*, Apa Apa (MSB 140720), Astillero (BMNH 1.6.7.30 [holotype of *ochrescens*]), Mapiri (AMNH 36490), Serranía Bella Vista (AMNH 246662, 246663), 13.7 km by road NE La Reserva (MSB 239309); *Santa Cruz*, Santa Cruz de la Sierra (BMNH 47.11.22.9 [lectotype of *boliviensis*]). **Brazil**—*Acre*, Igarapé Porongaba on Rio Juruá (MVZ 190350), Nova Vida on Rio Juruá (MVZ 190351), Ocidente on Rio Juruá (MVZ 190349), Rio Branco (AMNH 149145 [paratype of *iquiriensis*]). **Peru**—*Cusco*, Hacienda Cadena (FMNH 65673–65675, 66424, 68595, 68603, 78702), Ocobamba (BMNH 98.11.6.8 [holotype of *cuscinus*]; *Huánuco*, Aguas Calientes (FMNH 55407), Pozuzo (FMNH 24119), Tingo Maria (FMNH 242116); *Junín*, Chanchamayo (FMNH 65759–65762, 65764, 65765); *Loreto*, Pisqui River (AMNH 98437), Puerto Punga on Río Tapiche (AMNH 99203), Quebrada Pushaga (FMNH 88974–88980), Río Samiria (KU 140173), Río Tigre (FMNH 122952), Río Tigrillo (KU 140263, 140267–140269), Santa Luisa on Río Nanay (FMNH 87172), Sarayacu (AMNH 76325, 76326, 76442, 76444, 76466, 76467); *Madre de Dios*, Altamira (FMNH 98060–98063, 98065, 98066), Cuzco Amazónico (KU 144564, 144565), La Pampa (FMNH 52611 [holotype of *sanborni*]), Río Inambari (AMNH 16562, 37189, 37190); *Puno*, Inca Mines (AMNH 15803, 16560); *Ucayali*, Balta (MVZ 136571), Boca Río Urubamba (AMNH 75903), Lagarto on Río Ucayali (AMNH 78943), Santa Rosa on Río Ucayali (AMNH 75901), "Upper Ucayali" (BMNH 66.3.28.8–66.3.28.10 [syntypes of

irroratus, Gray, 1867])[8], Yarinacocha (FMNH 62085–62088), "Zona Pucallpa" (AMNH 147497).

Sciurus (*Hadrosciurus*) *pyrrhinus* Thomas, 1898

Figures 4A, 7A, 8B, 10B, 10E, 11B, 13

VOUCHER MATERIAL (*N* = 22): Jenaro Herrera (MUSM 23833), Marupa (AMNH 98430), Nuevo San Juan (AMNH 272859; MUSM 11192, 13354), Orosa (AMNH 73864, 73865, 73868, 73869, 73871–73874, 73877, 74057, 74059–74065).

UNVOUCHERED OBSERVATIONS: Choncó (Amanzo, 2006), Itia Tëbu (Amanzo, 2006), Río Yavarí (Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), San Pedro (Valqui, 1999, 2001).

IDENTIFICATION: Specimens and sightings of *Sciurus pyrrhinus* from our region have long been identified as *S. igniventris* (e.g., by Patton 1984; Salovaara et al., 2003; Amanzo, 2006; Sánchez-Vendizú et al., 2021). Although we follow Vivo and Carmignotto (2015) and Abreu et al. (2020b) by treating *S. pyrrhinus* and *S. igniventris* as distinct species, we are not convinced that they are consistently diagnosable morphologically. Additional analyses of sequence data and close study of pelage traits are needed to better document current taxonomic distinctions. As recognized in this report, *Sciurus pyrrhinus* is a geographically variable species that occurs north and south of the Amazon and includes the nominal taxa *cocalis* Thomas, 1900a, and *fulminatus* Thomas, 1926.

Specimens of *Sciurus pyrrhinus* from the Yavarí-Ucayali interfluve are large (645–715 g) squirrels that are uniformly grizzled reddish or reddish brown from crown to rump (none of the skins from our region are melanistic). Additionally, all examined specimens have bright orange postauricular patches (fig. 4A). The fore- and hind feet are always covered with self-orange fur, and the ventral pelage is uniformly pale orange. The fur at the base of the tail is often much darker than the dorsal body fur (almost blackish in some individuals), but the rest of the tail is conspicuously orange, although variously streaked or mottled with black in some specimens. Every examined parous female specimen with countable mammae in our material (*N* = 7) has eight teats.

Skulls of this species have a relatively short, broad rostrum and, like other members of the *Hadrosciurus* clade, only a single premolar in each upper cheektooth row. None of the specimens that we scored for cranial character variation has a distinct sagittal crest on the interparietal, and all of them have separate (not confluent) sphenopalatine and dorsal palatine foramina (fig. 7A). Additionally, most specimens (17 out of 18 scored) exhibit bilateral alisphenoid-parietal contact (AMNH 272859 has narrow squamosal-frontal contact on the right side), and most (13 of 19) have an accessory oval foramen on each side (six specimens lack this foramen on one or both sides). The sphenopalatine vacuities in the roof of the mesopterygoid fossa are very small or absent in all the specimens we examined.

The only other squirrel in our region with which *Sciurus pyrrhinus* could possibly be confused is *S. spadiceus*. Although these species are similar in size (table 7), they are easily distinguished with specimens in hand.[9] Red-phase specimens of *S. spadiceus* have much darker (sometimes almost blackish) fur on the crown of the head, lack conspicuous postauricular patches,

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[8] The type series of *Macroxus irroratus* was collected by E. Bartlett on the "Upper Ucayali" (Gray, 1867: 431). Thomas (1899: 40) remarked that these specimens were "probably from near Sarayacu" (a town on the Ucayali in modern Loreto department), but he cited no evidence for this inference, and none has come to light subsequently. In the absence of other indications, it would seem reasonable to assume that Bartlett's "Upper Ucayali" corresponds to the "Alto Ucayali" of Peruvian usage, a term that denotes the river above its confluence with the Río Pachitea, a left-bank tributary (Faura-Gaig, 1964: 287). This portion of the river lies entirely within the modern department of Ucayali. BMNH 66.3.28.8 is currently labelled as the lectotype, but we can find no published record that any of Gray's syntypes has been so designated.

[9] Field identifications of free-ranging individuals are more problematic, although blackish individuals in our region seem to always be *Sciurus spadiceus*.

FIG. 15. Ventral views of skins of *Sciurus pachecoi* (left three specimens: LSUMZ 28416; AMNH 75278, 74081) and *S. ignitus* (right three specimens: AMNH 76326; KU 140267, 140173) from Loreto department, Peru.

have grizzled-brownish (rather than self-orange) fore- and hind feet, and have more abundantly black-streaked tails. Skulls of *S. spadiceus* have longer and narrower rostrums than skulls of *S. pyrrhinus*, a difference that is visually obvious in side by side cranial comparisons (figs. 8, 10), and which is reflected in nonoverlapping measurements of diastemal length (LD, table 7). Additionally, in *S. spadiceus* the left and right temporalis scars usually converge to form a distinct sagittal crest on the interparietal bone (fig. 8A), the sphenopalatine and dorsal palatine foramina in the medial wall of the orbit are usually confluent (fig. 7B), and the sphenopalatine openings in the roof

of the mesopterygoid fossa are always large. On average, *S. spadiceus* has deeper lower incisors than *S. pyrrhinus*, although there is some species overlap in this dimension (DI, table 7).

Of the two subspecies of *Sciurus pyrrhinus* recognized by Vivo and Carmignotto (2015), our material closely resembles *S. p. fulminatus* in size and pelage traits based on our examination of the holotype (BMNH 20.7.1.1) and other specimens of *fulminatus*, which Thomas (1926) described from the lower Rio Negro, Amazonas state, Brazil. By contrast, our material differs from the type (BMNH 97.10.3.12) and other specimens of *S. p. pyrrhinus* from the Andean

TABLE 7

External and Craniodental Measurements (mm) of Giant Squirrels
(*Sciurus pyrrhinus* and *S. spadiceus*) from the Yavarí-Ucayali Interfluve

	S. pyrrhinus[a]	*S. spadiceus*[b]
HBL	272 ± 4 (268–278) 4	271 ± 11 (250–287) 14
LT	301 ± 10 (290–310) 3	266 ± 17 (228–290) 14
HF	69 ± 2 (65–75) 18	69 ± 2 (65–73) 36
Ear	34 ± 2 (31–35) 4	32 ± 1 (30–34) 14
CIL	57.4 ± 1.6 (54.4–59.7) 14	62.0 ± 1.6 (58.8–65.7) 37
LD	18.7 ± 0.8 (17.0–19.8) 19	21.5 ± 0.7 (20.1–23.3) 39
LIF	4.7 ± 0.4 (4.0–5.5) 19	4.8 ± 0.4 (4.0–5.9) 40
BIF	2.2 ± 0.2 (1.9–2.5) 19	2.0 ± 0.2 (1.8–2.4) 39
MTR	10.2 ± 0.3 (9.6–10.7) 19	10.0 ± 0.4 (9.2–10.7) 39
BM1	3.1 ± 0.1 (2.9–3.4) 19	3.2 ± 0.1 (2.9–3.5) 40
BPB	7.7 ± 0.5 (6.8–8.6) 19	7.2 ± 0.4 (6.0–7.9) 40
LN	20.3 ± 0.9 (19.3–23.0) 19	21.8 ± 1.2 (19.3–24.1) 40
BR	15.8 ± 1.0 (14.4–19.1) 19	14.5 ± 0.8 (12.8–16.6) 40
LIB	21.8 ± 0.8 (20.2–22.9) 19	21.8 ± 1.0 (18.7–23.5) 40
ZB	37.9 ± 1.1 (36.1–40.2) 17	39.2 ± 1.1 (35.8–41.4) 39
OW	14.0 ± 0.4 (13.4–14.6) 19	13.6 ± 0.4 (12.6–14.2) 39
DI	4.4 ± 0.2 (4.1–4.9) 19	5.2 ± 0.3 (4.6–5.8) 39

[a] The mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size for measurements of the following series: AMNH 73864, 73865, 73868, 73869, 73871–73874, 73877, 74057, 74058, 74060–74062, 74064, 74065, 98430, 272859; LSUMZ 28415; MUSM 13354, 23833.

[b] The mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size for measurements of the following series: AMNH 73863, 73866, 73867, 73870, 73875–73888, 74059, 74061, 74063, 98406, 98424, 98425, 98434, 98435, 268253, 272825, 272860; FMNH 87170, 87171, 88968–88973; LSUMZ 28413, 28415; MUSM 13355.

foothills of Junín department, Peru. The latter are smaller squirrels (HF ≤64 mm) with orange ventral fur that is mottled and streaked with white (two specimens, AMNH 63856 and 231771, have almost completely white underparts), they lack dark tail bases, and their caudal brush tends to be more thickly lined with black; additionally, some specimens (including the type) have black-based (rather than self-orange) fur on the fore- and hind feet. Consistent with these phenotypic comparisons, mitogenomes extracted from our voucher material (AMNH 272859, MUSM 13354) belong to the same haplogroup as sequenced specimens from the Brazilian state of Amazonas, whereas sequences extracted from specimens collected in Junín (including AMNH 231771) belong to a different haplogroup within the larger mtDNA clade that Abreu et al. (2020b: fig. 4C) identified as *S. pyrrhinus*. Therefore, if subspecific nomenclature were needed for these geographically variable squirrels, the appropriate trinomen for our material would be *S. p. fulminatus* according to the taxonomy suggested by Vivo and Carmignotto (2015). However, there is an older name that applies to the haplogroup to which our sequenced material belongs.

Sciurus cocalis was named by Thomas (1900a) based on several specimens from eastern Ecuador. The type (BMNH 0.6.3.4; from Coca, in Orellana province) is about the same size as our material (HF = ca. 67 mm) and has similarly grizzled-reddish dorsal fur, prominent postau-

ricular patches, self-orange fore- and hind feet, and a dark tail base; it differs from our material by having somewhat paler (buffy rather than orange) underparts, and it has a blackish lateral stripe separating the dorsal and ventral color zones. However, the blackish lateral stripe is not a constant feature of *cocalis*—as noted by Thomas (1900a)—and eastern Ecuadorean skins show a wide range of color variation, including some that are almost blackish dorsally (but not ventrally). Abreu et al. (2020b) obtained mtDNA sequence data from an eastern Ecuadorean specimen (AMNH 68271) that unambiguously associates the *cocalis* phenotype with the haplogroup that includes *fulminatus*-like specimens within the larger clade that they called *S. pyrrhinus*. Additional evidence that these phenotypes are conspecific comes from a large series collected by the Olallas at Boca Río Curaray (in northern Loreto department, Peru; fig. 1), which includes both *cocalis*-like skins (e.g., AMNH 72183, 72191), *fulminatus*-like skins (e.g., AMNH 72196, 72201), and others with intermediate pelage traits.

Vivo and Carmignotto (2015) regarded *cocalis* as a valid subspecies of *Sciurus igniventris*, but Abreu et al.'s (2020b) sequencing results suggest that *S. igniventris* is restricted to the upper Rio Negro region of northernmost Brazil and to the adjacent Orinoco basin of southern Venezuela and eastern Colombia. Squirrels from these regions in the AMNH have dorsal body fur that is heavily streaked with yellow and ventral pelage that is either deep reddish (in *S. i. igniventris*) or white (in *S. i. flammifer*). According to Vivo and Carmignotto's (2015) maps, the geographic ranges of *S. igniventris* and *S. pyrrhinus* overlap broadly in western Brazil, but Abreu et al.'s (2020b) results and our examination of museum skins suggest that these species are largely allopatric. A comprehensive revision of these giant squirrels is clearly needed to more convincingly establish geographic limits and to test alternative hypotheses about the validity of nominal taxa.

Ethnobiology: The Matses name kapa piu ("red squirrel") refers to *Sciurus pyrrhinus* and to the red phase of *S. spadiceus*, whereas kapa çhëşhë ("black squirrel") refers to the melanistic form of *S. spadiceus*. These folk taxa are thought to differ only in color and not in any other morphological or behavioral trait. In this account we will use the term "giant squirrel" to refer to both.

Giant squirrels are very minor game species for the Matses. When the Matses hunted with arrows, they would occasionally kill one, although they are not particularly fond of squirrel meat. Traditionally, only old people ate squirrel meat. Because giant squirrels are sometimes found low in the subcanopy, boys often used them for archery practice, and when they shot one it was gifted to a grandparent. Now that the Matses hunt with shotguns, hunters will not waste ammunition on a squirrel. Only children now hunt squirrels (with bows and arrows). Occasionally giant squirrels are kept as pets.

Matses natural History: These squirrels are red or black. They have a very bushy tail and large eyes. They have paired incisors, like those of an acouchy or a paca. Their incisors are strong and sharp enough to gnaw through the toughest palm nuts. Males have large testicles. They hold their tails over their heads while they eat. They have a strong scent, reminiscent of the smell of human milk. They may also smell like pinchuk palm (*Astrocaryum murumuru*) fruits.

Giant squirrels are found in all habitats, including primary and secondary forest, upland forest, and floodplain forest. They forage high or low in trees, and on the ground. They are encountered almost every day.

Giant squirrels make their nests from leaves and small branches up in the terminal branches of a tree. They also make nests in termite nests, in the crowns of pinchuk palms, and in the fruit clusters of budëd palm trees (*Attalea butyracea*). For giving birth, they line their nests with strips of bark.

Giant squirrels are diurnal. They sit right on the fruit bunches of budëd palms when they eat their fruits. They come down to the ground to feed on pinchuk palm fruits that have not yet ger-

minated. They can walk on the fronds of pinchuk palms without getting poked by the thorns. They pick dicot fruits from the branches and sit on large tree branches or spiraling vines to eat them. They also forage for dicot tree fruits and palm nuts on the ground. Several giant squirrels will gather to eat budëd fruits. After the young are weaned, they feed together with their mother.

Margays, hawks, and eagles eat giant squirrels. When giant squirrels see people or large animals (including predators) on the ground, they chatter, but do not run off. They hide on the opposite side of a tree when they see people.

They chatter saying "cododos" when they see a large animal or humans on the ground. They gnaw palm nuts loudly.

The principal food of giant squirrels is the endosperm of pinchuk palm nuts, which are abundant and available throughout the year. They also very commonly eat the endosperm of the nuts of other palms, including: budëd, shuinte mapi (*Attalea tessmanii*), dapais (*A. phalerata*), katsuin (*A. maripa*), antin (*A. septuagenata*), mio (*A. racemosa*), budëd uşhu (*A. microcarpa*), akte pinchuk (*Astrocaryum jauari*), and sinnaid (*Bactris* spp.). They also eat dicot tree fruits.

Remarks: All four specimens of *Sciurus pyrrhinus* accompanied by habitat information from our region were shot in the daytime by Matses hunters, three in primary floodplain (seasonally inundated) forest, and one in a palm swamp. The large series from Orosa was almost certainly collected in seasonally inundated forest, because the floodplain of the Amazon at this locality extends inland for some 15 km, of which perhaps the first 6–8 km closest to the river are seasonally inundated (Wiley, 2010: 40).

Matses observations about the natural history of giant squirrels (*Sciurus pyrrhinus* and *S. spadiceus*) are broadly consistent with the meager behavioral literature on these species (e.g., Eason, 2010; Gwinn et al., 2012; Palmer and Koprowski, 2014), particularly with respect to their role as the primary seed predators of palms in the genera *Astrocaryum* and *Attalea*.

Sciurus (*Hadrosciurus*) *spadiceus* (Olfers, 1818)

Figures 4B, 7B, 8A, 10C, 10F, 11C, 13

Voucher material (*N* = 41): Boca Río Yaquerana (FMNH 88969–88971), Bombo (AMNH 98424, 98425), Marupa (AMNH 98434, 98435), Nuevo San Juan (AMNH 268253, 272825, 272860; MUSM 13355), Orosa (AMNH 73863, 73866, 73867, 73870, 73875–73888, 74059, 74061, 74063), Quebrada Esperanza (FMNH 88972, 88973), Quebrada Vainilla (LSUMZ 28413, 28414), Río Blanco (AMNH 98406), San Fernando (FMNH 88967, 88968), Santa Cecilia (FMNH 87170, 87171). Additionally, Pavlinov (1994) reported three ZMMU specimens from Jenaro Herrera that we have not seen.

Unvouchered observations: Actiamë (Amanzo, 2006), Anguila (Escobedo-Torres, 2015), Chonkó (Amanzo, 2006), Divisor (Jorge and Velazco, 2006), Itia Tëbu (Amanzo, 2006), Río Yavarí (Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), Tapiche (Jorge and Velazco, 2006), San Pedro (Valqui, 1999, 2001).

Identification: *Sciurus spadiceus* is another large (540–683 g) squirrel, equivalent in size to sympatric *S. pyrrhinus*, but differing from that species in several external and craniodental traits (table 2). The most conspicuous difference is coloration: whereas *S. pyrrhinus* is consistently reddish in our region, most individuals of *S. spadiceus* (30 of 38 examined skins and fluid-preserved specimens) are melanistic, with black or grizzled-blackish fur. Red-phase individuals of *S. spadiceus* might be mistaken for *S. pyrrhinus* at a distance, but the crown of the head is darker in *S. spadiceus*, and postauricular patches are absent or indistinct (fig. 4B); additionally, the dorsal fur of red-phase *S. spadiceus* is duller and more conspicuously grizzled than that of *S. pyrrhinus*, and the distal limbs and feet are grizzled reddish rather than clear red or orange (fig. 13). As in other species in the subgenus *Hadrosciurus*, most females with countable mammae (*N* = 14) have eight teats (one fluid-preserved specimen, AMNH 272860, has seven).

Sciurus spadiceus has a visibly longer rostrum than other squirrels in our region (figs. 8, 10), and diastemal length (LD, table 7) is sufficient to distinguish skulls of this species from those of sympatric *S. pyrrhinus*. Additionally, the right and left temporalis scars converge to form a small but distinct sagittal crest on the interparietal of most specimens of *S. spadiceus* (29 of 32 scored for this character; fig. 8A), another unusual trait. Other distinctive cranial features include consistently large sphenopalatine vacuities in the roof of the mesopterygoid fossa and a large sphenopalatine foramen in the orbit that is usually confluent with the dorsal palatine foramen (in 37 of 40 specimens) and that usually exceeds the optic foramen in diameter (fig. 7B). An accessory oval foramen is present bilaterally in most specimens (33 of 37), and most specimens (33 of 40) exhibit bilateral alisphenoid-parietal contact. The lower incisors are remarkably deep in proportion to their width and, as in other species of the subgenus *Hadrosciurus*, only a single premolar is present in each upper cheektooth row.

Phylogenetic analyses of mtDNA sequences (Abreu et al., 2020b) suggest that *Sciurus spadiceus* exhibits little phylogeographic structure across its enormous geographic range, so it seems unlikely that the subspecies recognized by Vivo and Carmignotto (2015) are evolutionarily significant taxa. However, it is relevant to point out that the trinomial nomenclature proposed by those authors is based on the assumption that the type locality of *S. spadiceus* is in the Brazilian state of Mato Grosso, which cannot possibly be correct. Olfers (1818) based his description of *S. spadiceus* on ZMB material from Brazil, but the only specimens of Brazilian mammals in the ZMB collection prior to 1818 were either collected by Francisco Agostinho Gomes in the Atlantic Forest or by Friedrich Wilhelm Sieber in eastern Amazonia (Voss and Angermann, 1997). The likeliest place where Olfers' type material was collected—consistent with the geographic range of *S. spadiceus* (Vivo and Carmignotto, 2015: map 7) and Sieber's known itinerary

(Papavero, 1971: 48)—is somewhere along the right (south) bank of the Amazon west of the Tapajós or along the left (west) bank of the Tapajós itself. In fact, Olfers' (1818: 208) description[10] better fits the coloration of specimens from the lower Tapajós (in the AMNH) than that of specimens from Mato Grosso (as described by Vivo and Carmignotto, 2015). It is not known whether Olfers' type material still exists at the ZMB (C. Funk, personal commun.), but, if it cannot be found, a neotype should be selected to fix the application of this name.

ETHNOBIOLOGY: See the account for *Sciurus pyrrhinus* (above), which the Matses do not recognize as a different species.

MATSES NATURAL HISTORY: See the account for *Sciurus pyrrhinus* (above), which the Matses do not recognize as a different species.

REMARKS: The four specimens of *Sciurus spadiceus* accompanied by habitat information from our region were all shot in the daytime by Matses hunters. Of these, one was shot in secondary upland forest (probably an abandoned swidden), one was shot in a palm swamp, and two were shot in primary riparian (probably seasonally inundated) forest. As for *S. pachecoi* and *S. spadiceus* (see above), the large Orosa series was probably collected in seasonally inundated forest, but the specimens from Quebrada Vainilla were apparently taken in primary terra firme forest (Robbins et al., 1991).

Sciurus ("*Microsciurus*") *flaviventer* (Gray, 1867)

Figures 8D, 16

VOUCHER MATERIAL (*N* = 28): Boca Río Yaquerana (FMNH 88991–88893), Nuevo San Juan (AMNH 268250, 272819; MUSM 11188, 13307), Orosa (AMNH 73899–73912, 74074–74078), Quebrada Esperanza (FMNH 88994), San Fernando (FMNH 88990).

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[10] "Dorso et lateribus spadiceo nigroq. variis, capite superne obscuriore, abdomine albido, cauda nigro ferruginea, pilis nigris, apice ferrugineis." (Back and sides grizzled with brown and black, head rather dark on top, abdomen white, tail rusty black, the hairs black at their bases with rusty tips.)

Unvouchered observations: Actiamë (Amanzo, 2006), Anguila (Escobedo-Torres, 2015), Choncó (Amanzo, 2006), Divisor (Jorge and Velazco, 2006), Quebrada Pobreza (Escobedo-Torres, 2015), San Pedro (Valqui, 1999, 2001), Tapiche (Jorge and Velazco, 2006), Wiswincho (Escobedo-Torres, 2015).

Identification: The species referred to *Microsciurus* by Vivo and Carmignotto (2015) do not comprise a monophyletic group according to phylogenetic analyses of mitogenomes reported by Abreu et al. (2020b). Instead, these diminutive, small-eared, six-mammate sciurines with procumbent upper incisors and two upper premolars appear to belong to three separate lineages: (1) a pair of species (including the type species, *alfari* J.A. Allen, 1895, and an unnamed taxon ["species 1"]) restricted to Central America and western Colombia; (2) several species from Central America and the northern Andes (including *boquetensis* Nelson, 1903; *isthmius* Nelson, 1899; *mimulus* Thomas, 1898; *otinus* Thomas, 1901; and *similis* Nelson, 1899); and (3) three species from western Amazonia and the eastern Andes (including *flaviventer* Gray, 1867; *sabanillae* Anthony, 1922; and another unnamed taxon ["species 2"]). Each of these three clades is more closely related to larger squirrels traditionally referred to *Sciurus*, or to other sciurine genera, suggesting that the phenotype traditionally associated with *Microsciurus* has independently evolved several times (Abreu et al., 2020b).

Sciurus flaviventer is a widespread western Amazonian species. According to Vivo and Carmignotto (2015: map 8), this squirrel occurs in southeastern Colombia, eastern Ecuador, eastern Peru, and western Brazil. Mitogenomic sequences amplified from specimens identified as *S. flaviventer* within the geographic range mapped by Vivo and Carmignotto (2015) belong to two strongly supported haplogroups that occupy opposite sides of the Amazon, but these haplogroups are not known to be morphologically distinguishable, and species delimitation analyses suggest that they are conspecific (Abreu et al., 2020b). Unfortunately, the holotype of *S. flavi-* *venter* (BMNH 51.7.3.6) is a carelessly labelled Castlenau specimen from "Brazil," so it is not known whether this name properly applies to the northern or the southern haplogroup.[11] However, the type is morphometrically similar to our small series from the Yavarí-Ucayali interfluve (table 8), which it also resembles in other phenotypic traits. We have not attempted to assess the taxonomic status of the nominal taxa that Vivo and Carmignotto (2015) regarded as junior synonyms of *S. flaviventer*, none of which are from localities in or near our region.

In the Yavarí-Ucayali interfluve, *Sciurus flaviventer* is a small squirrel with very short (6–7 mm), uniformly grizzled-brownish or -olivaceous dorsal pelage. Most specimens have gray-based orange ventral fur, but some (e.g., AMNH 73900, 73903) have paler (gray-based buffy) fur on the chest or throat. The postauricular patches are pale buff or grayish, and the feet do not contrast in color with the dorsal body fur. The tail base is short furred and grizzled brownish like the rump, but the distal caudal fur appears frosted because the longer hairs have pale (buffy or grayish) tips. All examined parous female voucher specimens with countable mammae ($N = 4$) have six teats. Most adult specimens from our region are unaccompanied by external measurements, but AMNH 272819 measured 145 mm (HBL) × 130 mm (LT) × 41 mm (HF) × 18 mm (Ear), and weighed 100 g. Measurements of undistorted dried hind feet that we obtained from another six specimens ranged from 38 to 42 mm.

Skulls of this species lack a sagittal crest, the squamosal and frontal are in contact on the lateral braincase, and an accessory oval foramen is usually absent (three specimens that we examined exhibit this opening unilaterally). The sphenopalatine and dorsal palatine foramina are separate, and sphenopalatine vacuities in the roof of the mesopterygoid fossa are very small or absent. The upper incisors are conspicuously

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[11] François-Louis Laporte, comte de Castelnau, was a French naturalist whose travels in Brazil from 1843 to 1847 included a descent of the Amazon with abundant opportunities for collecting on both banks of the river (Papavero, 1971).

TABLE 8

Craniodental Measurements (mm) of *Sciurus flaviventer*

	BMNH 51.7.3.6[a]	Yavarí-Ucayali sample[b]
CIL	—	32.6 ± 0.6 (31.7–33.3) 11
LD	10.0	8.8 ± 0.3 (8.0–9.1) 10
LIF	2.1	2.2 ± 0.2 (1.7–2.5) 12
BIF	1.7	1.5 ± 0.2 (1.3–1.8) 12
MTR	6.6	6.2 ± 0.2 (6.0–6.8) 10
BM1	1.9	1.7 ± 0.1 (1.5–1.8) 12
BPB	5.7	5.4 ± 0.2 (5.0–5.8) 10
LN	10.6	10.1 ± 0.3 (9.3–10.6) 12
BR	11.2	11.2 ± 0.5 (10.6–12.4) 12
LIB	13.8	13.6 ± 0.5 (12.9–14.4) 12
ZB	—	22.7 ± 0.8 (21.8–23.9) 7
OW	8.9	9.0 ± 0.2 (8.6–9.2) 10
DI	2.1	1.9 ± 0.1 (1.8–2.0) 12

[a] The holotype, an old adult from "Brazil" (see text).
[b] The mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size for measurements of the following series: AMNH 73900, 73902, 73904, 73906, 73907, 73909, 73910, 74075, 74076, 74078, 272819; MUSM 11188.

procumbent (proodont sensu Thomas, 1919), and two premolars are consistently present in each upper cheektooth row.

Sciurus flaviventer appears to be the only species of *Microsciurus* (sensu lato) in the Amazonian lowlands. Abreu et al. (2020b: fig. 5) mapped a western Amazonian lowland locality for the species they called "*Microsciurus*" *sabanillae* based on a sequenced specimen from a Peruvian locality called Santa Rosa (AMNH 69238), but the geographic coordinates they assigned to this locality were incorrect.[12] The same authors also mapped several western Amazonian localities for "*Microsciurus* species 2," but the only corresponding voucher specimen we were able to examine (KU 144565) is morphologically indistinguishable from *Sciurus ignitus*; this case of genotype/phenotype discordance is apparently not the result of lab error and is currently being investigated (E.F. Abreu, personal commun.).

ETHNOBIOLOGY: The Matses name for the dwarf squirrel is kapa kudu ("gray squirrel"). The Matses do not recognize any subtypes and have no synonymous names for this species. Some Matses confuse it with the pygmy squirrel or with Pacheco's squirrel.

The dwarf squirrel has no economic importance for the Matses. They are sometimes kept as pets.

MATSES NATURAL HISTORY: The dwarf squirrel is similar in form to the pygmy squirrel, but it is a bit larger and more reddish.

The dwarf squirrel is found in all habitats. The Matses see them infrequently when they are in the forest.

It makes its nest in hollowed-out termite nests and lines its nest with strips of bark.

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[12] AMNH 69238 was collected by Harry Watkins in 1924. Based on Watkin's archived correspondence with AMNH ornithology curator Frank M. Chapman, the locality called Santa Rosa where Watkins collected in 1924 can be definitely placed in Cajamarca department at 5.43°S, 78.57°W. According to the same source, Watkins' altimeter reading at Santa Rosa was 3900 ft (1189 m). The erroneous coordinates that Abreu et al. (2020b: fig. 5) used for mapping this locality were obtained from an AMNH database wherein Watkin's Santa Rosa was misidentified as an Olalla locality of the same name in Loreto department.

FIG. 16. Dorsal, ventral, and lateral cranial views of *Sciurus flaviventer* (AMNH 268250, a subadult specimen). All views about ×2.0.

Sometimes two are found together.

They eat small dicot tree fruits and the endosperm of <u>pinchuk</u> palm (*Astrocaryum murumuru*) nuts.

REMARKS: The four specimens of *Sciurus flaviventer* accompanied by habitat data from our region were all shot by Matses hunters. Of these, three were collected in primary upland (terra firme) forest and one in riparian (probably seasonally inundated) forest. As for other squirrels collected by the Olallas at Orosa (see above), the large series of *S. flaviventer* from that locality were probably taken in seasonally flooded forest.

The Matses notion that this small squirrel, with its delicate, procumbent incisors, is capable of gnawing through the very hard, thick shells of *Astrocaryum* nuts is implausible. Additionally, its allegedly frugivorous/granivorous diet seems inconsistent with the previously reported behavior of this species, which is said to forage "apparently for arthropods, by searching actively over large trunks, vines, and treefalls," and to scrape an unknown substance from the bark of large trees (Emmons, 1997). Because the Matses (by their own admission) seldom see this species, it is likely that they attribute to it the characteristic behaviors of larger squirrels that they observe more frequently.

Cricetidae

All the cricetids known to occur in the Yavarí-Ucayali interfluve are members of the sigmodontine tribe Oryzomyini, although members of other sigmodontine tribes could also be expected in our region (appendix 5). Oryzomyine taxonomy has undergone major transformations in the past few decades, both from species-level revisionary work (e.g., Musser et al., 1998) and from phylogenetic analyses and subsequent generic reclassifications (Weksler, 2003, 2006, 2015; Weksler et al., 2006). Among other noteworthy changes, the genus *Oryzomys*, a formerly polyphyletic taxon that included many Amazonian species, is now restricted to a much smaller number of mostly trans-Andean taxa. Except as noted otherwise below, oryzomyine taxonomy in this report follows Patton et al. (2015), which includes morphological diagnoses and keys to all the genera mentioned in the following accounts (*Amphinectomys*, *Euryoryzomys*, *Holochilus*, *Hylaeamys*, *Neacomys*, *Nectomys*, *Oecomys*, *Oligoryzomys*, and *Scolomys*).

Cricetid taxonomy is an active field of research, and the literature can be daunting for newcomers. Nevertheless, the following accounts assume familiarity with cricetid comparative morphology, including terminology for aspects of external and craniodental anatomy defined or referenced by Voss (1988) and Weksler (2006). Although we devote much attention to external features that might be useful for field identifications, it must be emphasized that many cricetids in our region cannot be confidently identified to species without collected voucher material.

MEASUREMENTS: We measured the following dimensions of cricetid skulls and teeth (fig. 17):

CIL, condyloincisive length: from the greater curvature of one upper incisor to the articular surface of the occipital condyle on the same side.

LD, length of diastema: from the lesser curvature of an upper incisor to the crown of the first upper molar (M1).

LM, length of molars: greatest crown length of the upper molar row (from M1 to M3).

BM1, breadth of M1: greatest transverse dimension of the crown of either the left or right first upper molar.

LIF, length of incisive foramen: greatest anterior-posterior dimension of either the left or right incisive foramen.

BIF, breadth of incisive foramina: greatest transverse dimension across both foramina.

BPB, breadth of palatal bridge: breadth of the palate between the crowns of the right and left first upper molars.

BZP, breadth of the zygomatic plate: least width of the zygomatic plate from its anterior to posterior margins.

LIB, least interorbital breadth: the least transverse dimension between the orbits across the frontal bones.
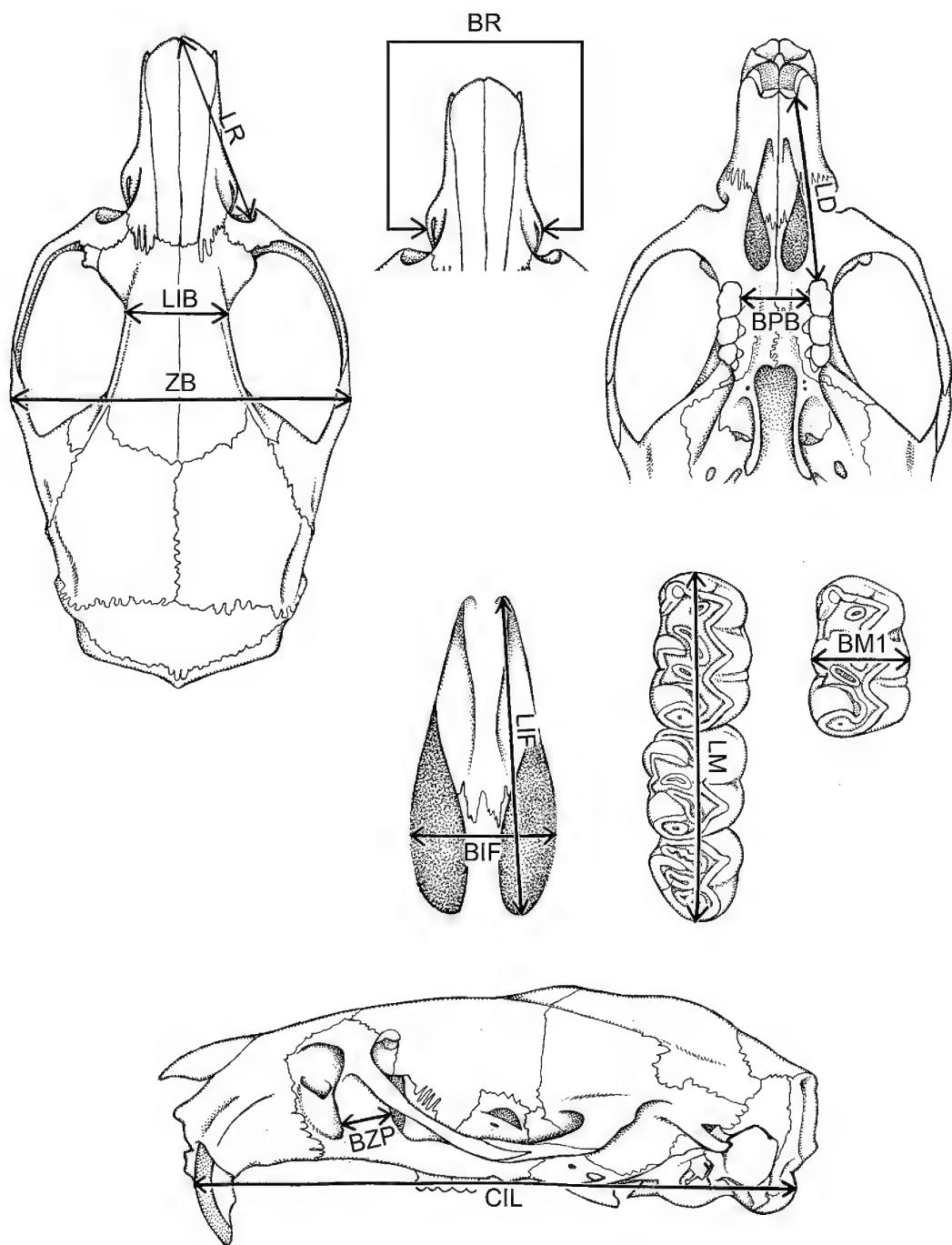
FIG. 17. Limits of 12 cricetid craniodental measurements defined in the text.

ZB, zygomatic breadth: the greatest transverse dimension across the zygomatic arches.

BR, breadth of rostrum: the greatest transverse dimension across the undamaged nasolacrimal capsules.

LR, length of rostrum: distance from the distal apex of an intact nasal bone to the posterior margin of the ipsilateral zygomatic notch.

AGE DETERMINATION: The last teeth to erupt in cricetids are the third molars (M3/m3), but specimens with fully erupted dentitions can exhibit statistically significant and visually conspicuous ontogenetic variation in cranial size and shape (e.g., Voss, 1991: fig. 16). To minimize the confounding effect of such ontogenetic variation for morphometric comparisons, we recorded measurement data from specimens with visible wear (exposed dentine) on all of the cusps and crests of M3. We refer to such specimens as "adults" without any intended implication of reproductive maturity.

ETHNOBIOLOGY: The cricetids that occur in our region are all small (<300 g), nocturnal, and generally inconspicuous. Not surprisingly, the Matses consistently distinguish only a few by name, either because they are occasionally trapped and eaten, or because they are semicommensal pests. The term tambisëmpi ("little paca") can refer specifically to echimyid spiny rats (*Proechimys* spp.), but it is also used as a general term that includes all rats and mice in the families Echimyidae and Cricetidae. The term maka ("mouse/rat") is an old word that presumably has (or had) the same meaning as the general sense of tambisëmpi, but it currently survives only as part of the names of three folk species: maka tanun ("gray rat," for *Nectomys apicalis*), abuk maka ("up rat," for arboreal echimyids), and abuk makampi ("little up rat," for species of the arboreal cricetid genus *Oecomys*). In effect, the Matses folk classification system does not distinguish these two rodent families.

Another Matses folk-taxon name associated with cricetids is takbid umu ("gray belly"). This term apparently refers to any mouse-size rodent with grayish ventral fur (such as *Hylaeamys*

spp.), but it is difficult to ascertain precisely the full semantic range of this term. A regional variant name for this folk category is takbid çhëşhë ("black/dark-colored belly"). These species may also be referred to as cheka, which is a term that prototypically designates opossums, but in more general usage includes any small rodent that is not eaten (e.g., all cricetids except *Nectomys apicalis*) as well as an unidentified species of climbing rat mysteriously known as yama.[13]

Lastly, the Matses refer to a rodent called şhëa that we are unable to identify. Like the semicommensal species known as şhubu pekid (*Oecomys bicolor*; see below), şhëa is said to be a pest that takes up residence in Matses houses, feeds on maize and other food, and chews noisily on thatch, where it makes its nest. However, several Matses claim that they have not seen one for several decades, so it is possible that şhëa lived only in traditional Matses longhouses (which were thatched all the way to the ground) and do not enter modern Matses homes (which are built on stilts). According to the Matses, şhëa is a tiny mouse (smaller than *O. bicolor*) with grayish dorsal fur, a white belly, large ears, and a long tail. Neither this physical description nor details of its alleged behavior (e.g., arboreal locomotion, foraging for fruit in the forest) are a compelling match for any local species known to us.

Amphinectomys savamis Malygin 1994

Figures 18A, 18D

VOUCHER MATERIAL (*N* = 5): Jenaro Herrera (ZMMU S-155533 [the holotype, not seen]), San Pedro (UF 30466, MUSM 22334), Quebrada Sábalo (MUSA 15219 [not seen]), Quebrada Lobo (MUSA 15110 [not seen]).

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[13] The term yama has three distinct meanings. It designates short-tailed opossums (*Monodelphis* spp.), turnip-tailed geckos (*Thecadactylus rapicaudus*), and a species of arboreal rat that we have not been able to capture. The latter is described by the Matses as having reddish dorsal fur and a white belly, traits that do not quite fit any species known or expected to occur in the region. The magical properties attributed to yama rats were described by Voss et al. (2019: 34).
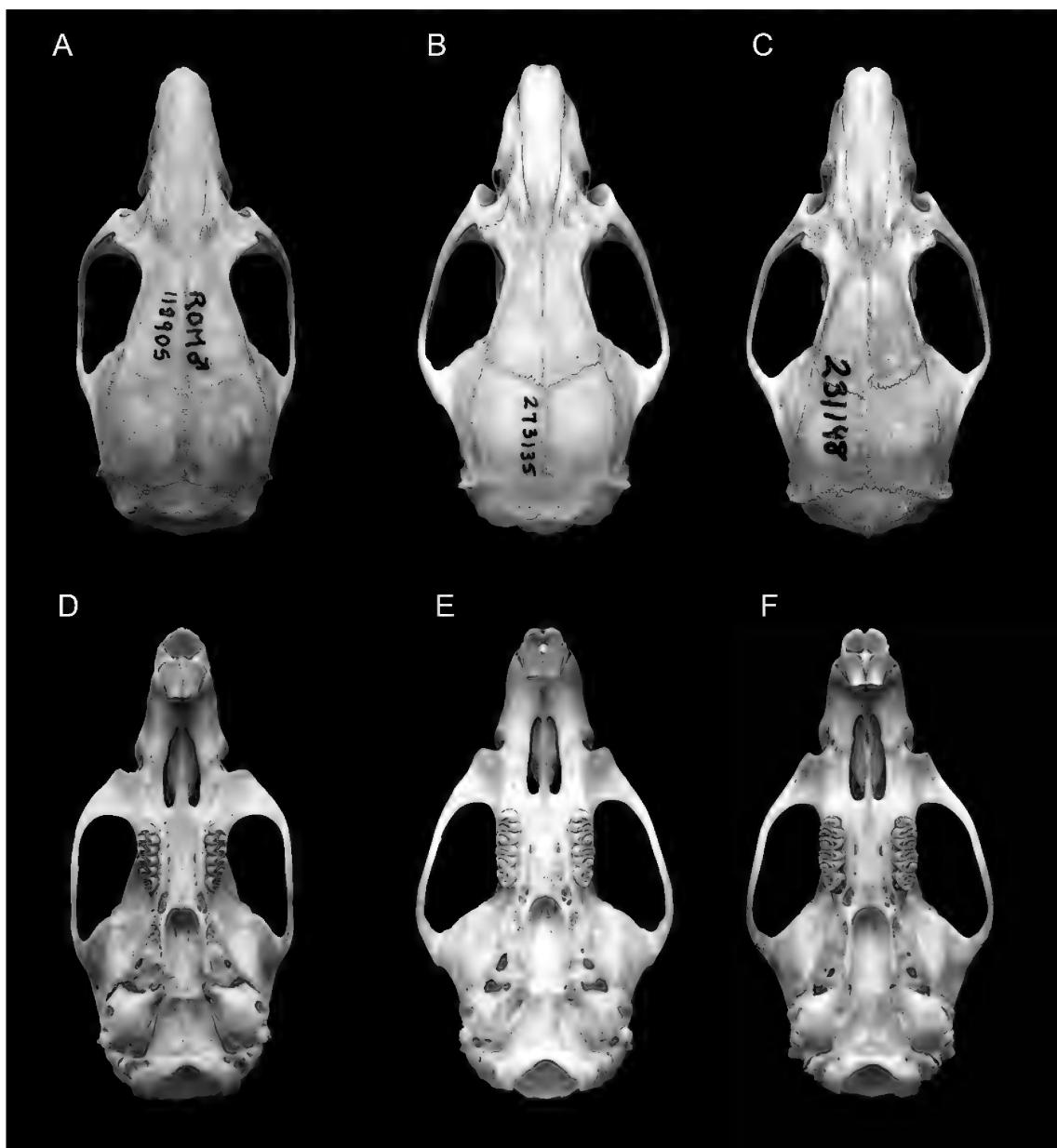
FIG. 18. Dorsal and ventral cranial views of *Amphinectomys savamis* (**A**, **D**; ROM 118905), *Nectomys apicalis* (**B**, **E**; AMNH 273135), and *N. rattus* (**C**, **F**; AMNH 231148). The skulls of *A. savamis* and *N. rattus* are not from the Yavarí-Ucayali interfluve. All views about ×1.5.

TABLE 9

Morphological Comparisons between *Amphinectomys savamis* and Sympatric Species of *Nectomys*

	Amphinectomys savamis	*Nectomys* spp.[a]
Dorsal fur length	18–20 mm	10–12 mm
Ventral pelage	gray-based whitish	gray-based buffy
Mystacial vibrissae	long (extending well behind pinnae)	short (not extending behind pinnae)
Interdigital webbing on hind foot	extends to base of claws	extends only between 1st phalanges
Posterior margin of nasals	bluntly rounded	acutely pointed
Sphenopalatine vacuities	present	absent or very small
Upper molars	low crowned, not lophodont	higher crowned, lophodont

[a] *Nectomys apicalis* and *N. rattus*.

UNVOUCHERED OBSERVATIONS: None.

OTHER SPECIMENS EXAMINED (*N* = 4): **Ecuador**—*Orellana*, 35 km S Pompeya Sur (ROM 105944), 46 km S Pompeya Sur (ROM 118901, 118905), 76 km S Pompeya Sur (ROM 106057).

IDENTIFICATION: This semiaquatic cricetid species was originally described from a single specimen trapped by a Soviet research team at Jenaro Hererra, but additional specimens have subsequently been discovered in museums or collected at other localities. Previously known only from the Yavarí-Ucayali interfluve (Malygin et al., 1994; Valqui, 1999; Medina et al., 2015; Weksler and Valqui, 2015), *Amphinectomys savamis* was recently reported from eastern Ecuador based on an old specimen in the Muséum National d'Histoire Naturelle (Chiquito and Percequillo, 2017), and we later identified additional specimens from eastern Ecuador in the Royal Ontario Museum (see above). Because the species occurs on both sides of the upper Amazon and is probably not confined by other rivers in western Amazonia, we expect that it will eventually be found to occupy a wider geographic range, perhaps including southeastern Colombia and western Brazil.

Amphinectomys morphologically resembles *Nectomys* and, indeed, the two genera are closely related (Weksler, 2006; Weksler and Valqui, 2015). In external appearance, *Amphinectomys* and *Nectomys* are large (>100 g) rats with small ears (not reaching the eye when folded forward) and large, webbed hind feet that have visibly scaly soles. Despite such resemblances, *Amphinectomys* can easily be identified in the field with specimens in hand (table 9). Among other external differences, *Amphinectomys* has much longer dorsal fur than *Nectomys*, whitish (versus buffy) ventral fur, much longer mystacial vibrissae, and much more extensive interdigital webbing on the hind feet.[14] Craniodental traits are also diagnostic: *Amphinectomys* has nasal bones with bluntly rounded (versus acutely pointed) posterior margins, and small (versus absent or indistinct) sphenopalatine vacuities. The molars of *Amphinectomys* are lower crowned and differ in occlusal morphology from those of *Nectomys*: whereas the molars of *Nectomys* are lophodont (with interpenetrating labial and lingual flexi), the labial and lingual flexi of *Amphinectomys* do not extend beyond the midline of the tooth and do not interpenetrate. Other generic differences were described by Chiquito and Percequillo (2017), whose online supplemental information includes photographs of the skin and molars of *A. savamis*.

Morphometric variation among specimens of *Amphinectomys savamis* from Peru and Ecuador (table 10) is well within the range of

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[14] Contra Weksler and Valqui (2015: 298), the manus (forefoot) is not webbed.

TABLE 10

External and Craniodental Measurements (mm) and Weights (g) of *Amphinectomys savamis*

	Yavarí-Ucayali (Peru)			Eastern Ecuador					
	ZMMU 155533[a]	MUSM 22334	MUSA 15110[b]	MNHN 1932-2940[c]	ROM 105944	ROM 106057	ROM 118901	ROM 118905	Combined sample[d]
HBL	190	187	168	202	207	191	190	202	192 ± 13
LT	206	173	169	205	215	190	—	200	194 ± 17
HF	54	53	49	48	56	53	53	52	52 ± 3
Ear	24	24	21	23	24	24	24	23	23 ± 1
CIL	39.0	38.8	36.1	41.8	43.0	40.2	38.5	40.2	39.7 ± 2.1
LD	10.9	11.4	10.2	12.2	13.1	11.4	11.0	11.9	11.5 ± 0.9
LM	6.5	6.3	6.4	6.9	—	6.9	6.4	6.4	6.6 ± 0.2
BM1	2.2	2.1	2.0	2.3	—	2.2	2.1	2.1	2.1 ± 0.1
LIF	6.8	6.8	6.3	7.0	7.6	6.6	6.9	7.3	6.9 ± 0.4
BIF	3.2	3.4	3.0	3.2	3.5	3.3	3.1	3.4	3.3 ± 0.2
BPB	—	4.0	3.5	—	4.3	3.9	3.9	4.0	4.5 ± 1.1
BZP	4.3	4.4	3.9	5.3	5.0	4.3	3.9	4.4	4.4 ± 0.5
LIB	8.1	7.9	7.5	8.9	7.6	8.2	8.1	8.0	8.1 ± 0.4
ZB	20.8	—	19.2	—	22.8	20.8	20.8	20.6	20.8 ± 1.1
LR	—	15.1	—	—	17.3	15.3	14.2	15.5	15.5 ± 1.1
Weight	214	225	135	—	210	206	217	200	201 ± 30

[a] The holotype. External measurements from Malygin et al. (1994); craniodental measurements from Elisandra Chiquito (personal commun., 27 February 2023).
[b] Measurements from Medina et al. (2015) and Horacio Zeballos (personal commun., 21 February 2023).
[c] Measurements from Elisandra Chiquito (personal commun., 27 February 2023).
[d] The mean plus or minus one standard deviation.

variation that could be expected for conspecific material. Chiquito and Percequillo (2017) interpreted the few differences they observed between their Ecuadorean specimen and the Peruvian holotype as intraspecific variation, and we agree. For example, among the four ROM specimens we examined from Orellana province, Ecuador, there is variation in nasal length and subsquamosal fenestra expression similar to the differences that Chiquito and Percequillo observed between MNHN 1932-2940 and ZMMU S-155533. Like those authors, we conclude that there is no compelling evidence for multiple species of *Amphinectomys*.

ETHNOBIOLOGY: This species is not known to the Matses, who have no special name for it.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: The specimen from Jenaro Herrera was trapped on the bank of a small stream in primary forest, as was one of the specimens from San Pedro (Weksler and Valqui, 2015). The specimens from Quebrada Lobo and Quebrada Sábalo were both taken in pitfall traplines that crossed small streams in primary forest (Medina et al., 2015). Of eight specimens collected by ROM researchers in eastern Ecuador, three were trapped along a stream in primary upland forest, one was trapped along a muddy streambed in unrecorded habitat, and four were trapped along the edge of a stream in a habitat described as "semi-inundated forest" (B.K. Lim, personal commun., 27 February 2023).

We hypothesize that *Amphinectomys savamis* is primarily associated with seasonally flooded forests, despite the fact that it has not been collected in such habitats, which are prohibitively difficult to trap during the season of high water. This inference is based on its completely webbed hind feet, which would be an asset in environments lacking terrestrial substrate for much of the year, and on its apparently restricted distribution in western Amazonia, where flooded forests are more common than in eastern Amazonia. All the watercourses in which this species is known to have been trapped are tributaries of rivers flanked by seasonally flooded forest, and it seems likely that *Amphinectomys* retreats into upland streams when the waters recede from the floodplain.

Euryoryzomys macconnelli (Thomas, 1910)

Figures 19A, 19D

Voucher material (*N* = 35): Jenaro Herrera (MUSM 16004), Nuevo San Juan (AMNH 268260, 272669, 272675, 272678, 272694, 272696, 272701–272703, 272711, 273100; MUSM 13321–13325, 13333–13336, 15341, 15342), San Pedro (UF 30485, 30486, 30491, 30493–30495, 30497–30500, 30504, 30505). Additional specimens that we have not examined were reported by Pavlinov (1994) from Jenaro Herera and by Medina et al. (2015) from Quebrada Betilia and Quebrada Lobo.

Unvouchered observations: None.

Identification: As currently understood, *Euryoryzomys macconnelli* (formerly *Oryzomys macconnelli*; see Weksler et al., 2006) is a widespread Amazonian species that ranges from the Atlantic Ocean to the base of the Andes on both sides of the Amazon River (Percequillo, 2015a). Although Musser et al. (1998) did not discover any noteworthy geographic variation in morphology among the population samples they examined, Patton et al. (2000) reported phylogenetic analyses of cytochrome *b* sequence data that suggest the existence of several highly divergent mtDNA lineages, each of which is associated with a different karyotype; these authors recognized a northeastern clade with $2n = 76$ chromosomes, a northwestern clade with $2n = 58$, and a southern clade with $2n = 64$. The type locality of *E. macconnelli* is in Guyana, so Patton et al.'s northeastern clade would presumably correspond to the nominotypical form (if a trinomial classification were adopted) or to the species in some appropriately restricted sense (if other species were to be recognized in this complex).

Specimens from the Yavarí-Ucayali interfluve closely resemble *Euryoryzomys macconnelli* as described in detail by Musser et al. (1998: 227–232). Additionally, measurements of our specimens (table 11) broadly overlap measurements of the type series (Voss et al., 2001: table 33). Despite such qualitative and metrical similarity, an unpublished molecular analysis recently found that cytochrome *b* sequences obtained from several of our vouchers (AMNH 272669, 272678, 272694; MUSM 13321, 13333) differ from topotypical sequences by >8% (Martínez, 2021). Although it seems likely that multiple taxa are represented among the geographic forms currently identified as *E. macconnelli*, we are currently unable to distinguish them morphologically. Additionally, because the available molecular data were obtained from a single mitochondrial gene, and because only a few specimens from widely scattered localities have been karyotyped, we prefer to maintain traditional binomial usage until a formal taxonomic revision is feasible.

Euryoryzomys macconnelli somewhat resembles two sympatric species of *Hylaeamys*, with which it might be confused. These three species have overlapping measurements (table 11), and they all have soft (nonspinous) fur; large ears (reaching the eye when folded forward); long, narrow hindfeet with unwebbed digits; dense ungual tufts that conceal the claws; and macroscopically naked tails. In dorsal cranial view (fig. 19) they all have long rostrums; deep zygomatic notches; and beaded, anteriorly convergent interorbital regions. In ventral cranial view, they have short incisive foramina; long/wide palates; low-
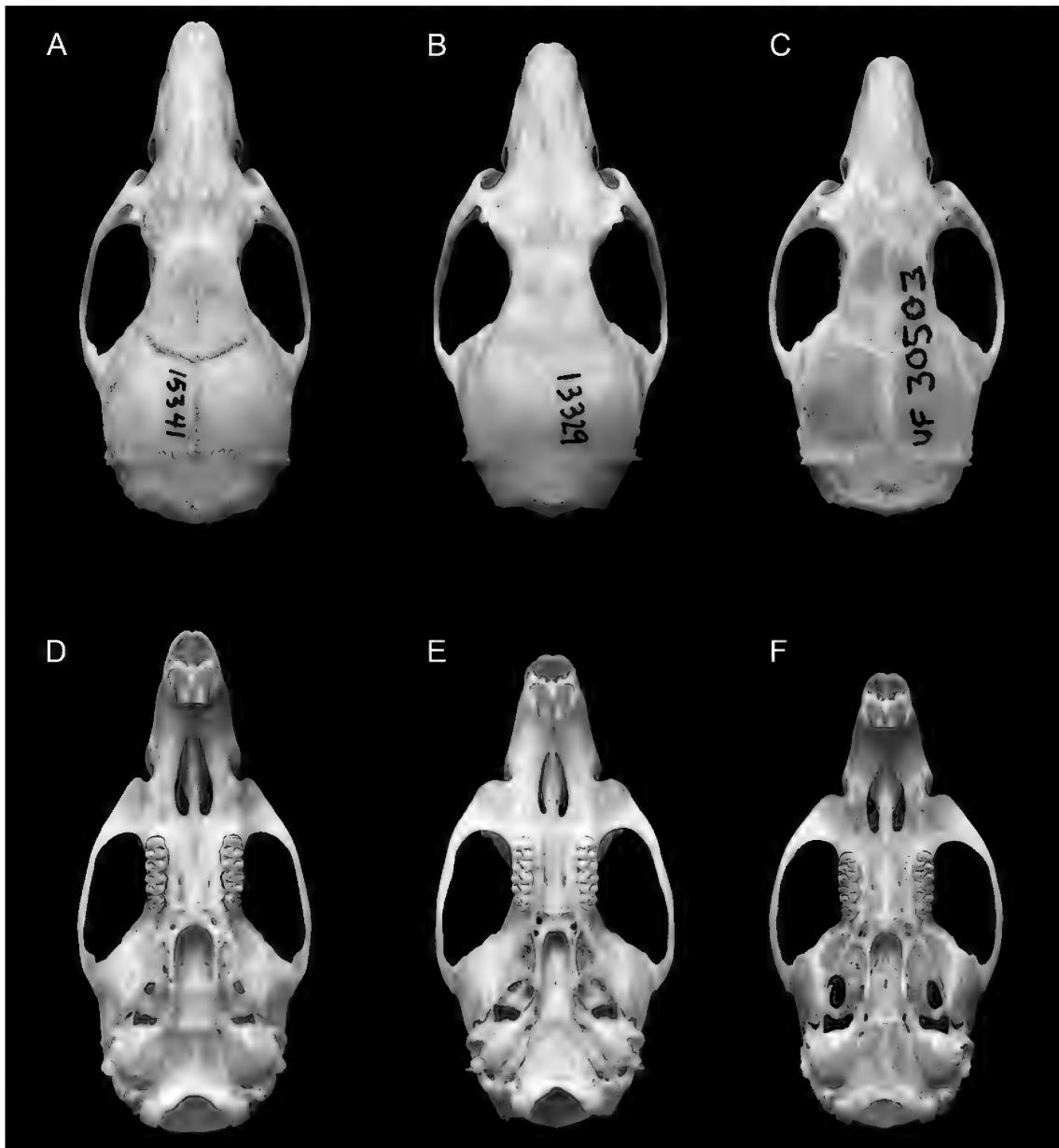
FIG. 19. Dorsal and ventral cranial views of *Euryoryzomys macconnelli* (**A, D**; MUSM 15341), *Hylaeamys perenensis* (**B, E**; MUSM 13329), and *H. yunganus* (**C, F**; UF 30503). All views about ×2.0.

crowned, pentalophodont molars; narrow parapterygoid fossae; and small auditory bullae. Nevertheless, several morphological characters unambiguously distinguish *Euryoryzomys* from *Hylaeamys* (table 12) such that vouchered generic identifications can be made with confidence.

ETHNOBIOLOGY: This species is not known to the Matses, who have no special name for it.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: Of 22 specimens of *Euryoryzomys macconnelli* accompanied by ecological informa-

TABLE 11

External and Craniodental Measurements (mm) and Weights (g) of *Euryoryzomys macconnelli*, *Hylaeamys perenensis*, and *H. yunganus* from the Yavarí-Ucayali Interfluve

	E. macconnelli[a]	*H. perenensis*[b]	*H. yunganus*[c]
HBL	138 ± 11 (120–161) 17	136 ± 9 (122–150) 15	121 ± 7 (112–128) 9
LT	142 ± 13 (120–162) 17	123 ± 8 (106–143) 15	98 ± 10 (85–115) 9
HF	34 ± 2 (31–37) 21	32 ± 2 (29–34) 15	28 ± 2 (25–30) 10
Ear	23 ± 2 (20–27) 17	21 ± 1 (19–23) 14	18 ± 1 (17–21) 6
CIL	30.4 ± 1.2 (27.7–32.6) 22	29.6 ± 1.4 (27.6–32.2) 15	28.1 ± 0.9 (26.7–29.5) 10
LD	9.0 ± 0.5 (8.0–10.0) 22	8.7 ± 0.6 (8.0–9.9) 15	8.2 ± 0.4 (7.5–8.8) 10
LM	5.2 ± 0.2 (4.9–5.4) 22	5.1 ± 0.2 (4.5–5.5) 22	4.8 ± 0.1 (4.6–5.0) 11
BM1	1.5 ± 0.1 (1.4–1.6) 22	1.4 ± 0.1 (1.3–1.6) 23	1.5 ± 0.0 (1.5–1.6) 11
LIF	5.1 ± 0.4 (4.3–6.0) 22	4.6 ± 0.4 (4.0–5.4) 15	4.5 ± 0.3 (3.7–4.9) 10
BIF	2.6 ± 0.3 (1.9–3.1) 22	2.3 ± 0.2 (1.9–2.5) 15	2.3 ± 0.2 (1.9–2.7) 10
BPB	3.4 ± 0.2 (3.1–3.9) 22	3.1 ± 0.2 (2.7–3.5) 15	3.2 ± 0.2 (2.8–3.5) 10
BZP	3.4 ± 0.3 (2.8–4.0) 22	3.5 ± 0.3 (3.0–4.1) 15	3.5 ± 0.2 (3.2–3.9) 10
LIB	5.5 ± 0.2 (5.1–6.2) 22	5.4 ± 0.2 (5.0–5.8) 15	5.0 ± 0.2 (4.6–5.3) 10
ZB	16.2 ± 0.6 (15.2–17.5) 20	16.2 ± 0.7 (14.6–17.3) 15	16.0 ± 0.2 (15.6–16.3) 9
LR	12.2 ± 0.5 (11.3–13.0) 22	11.3 ± 0.7 (10.1–12.8) 15	10.2 ± 0.5 (9.4–11.4) 10
Weight	79 ± 10 (65–96) 20	64 ± 11 (49–83) 12	57 ± 8 (45–67) 8

[a] The mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size for measurements of the following series: AMNH 272669, 272678, 272694, 272701, 272711, 273100; MUSM 13322, 13324, 13333, 15341, 15342; UF 30485, 30486, 30491, 30493, 30495, 30497–30500, 30504, 30505.

[b] The mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size for measurements of the following series: AMNH 73829–73832, 74095–74097, 268261, 272688, 272713, 271718, 272826, 273065; MUSM 13326, 13327, 13329–13331, 15343, 15345; UF 30508, 30509, 30517, 30518.

[c] The mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size for measurements of the following series: MUSM 11221, 13332; UF 30483, 30583, 30526, 30528, 30535, 30540, 30541, 30543, 30545.

tion from our region, all were collected in well-drained primary forest; none was collected or observed in secondary vegetation or in floodplain forest. Most specimens (*N* = 20) were trapped on the ground, usually under sheltering understory vegetation, but occasionally out in the open, and once inside a hollow log; trapped specimens were taken in moist valley bottoms, but also on hillsides and ridge crests. Additionally, one specimen was shot on the ground, and another was shot by a Matses hunter as it perched "not very high up" on a liana. These capture data from the Yavarí-Ucayali interfluve are consistent with previous observations from other Amazonian inventory sites that *E. macconnelli* is a terrestrial species that strongly prefers primary upland forest (Musser et al., 1998; Patton et al., 2000).

Holochilus nanus Thomas, 1897

Figure 20

VOUCHER MATERIAL (*N* = 13): Orosa (AMNH 73816–73828).

UNVOUCHERED OBSERVATIONS: Jenaro Herrera (Aniskin, 1994).

IDENTIFICATION: Species of *Holochilus*, commonly known as marsh rats, occur in cis-Andean open wetlands from Colombia, Venezuela, and the Guianas southward to northern Argentina. The current taxonomy (Prado et al., 2021a) rec-

TABLE 12

Morphological Comparisons between *Euryoryzomys macconnelli* and Sympatric Species of *Hylaeamys*

	Euryoryzomys macconnelli	*Hylaeamys* spp.
Dorsal pelage length	12–16 mm	7–9 mm
Dorsal pelage color	bright tawny to reddish brown	usually dull, dark brown
LT/HBL × 100[a]	ca. 100%	ca. 80%–90%
Tail coloration	distinctly bicolored	indistinctly bicolored or unicolored
Carotid circulation[b]	pattern 1	pattern 2
Mastoid capsules[c]	not fenestrated	fenestrated

[a] Average ratio of tail to head-and-body length, expressed as a percentage.
[b] A supraorbital branch of the stapedial artery is present in taxa with pattern 1 but absent in taxa with pattern 2 (Voss, 1988: fig. 18).
[c] The occipital exposure of pars mastoideus of the petrosal (Weksler, 2006: char. 43, fig. 22).

ognizes seven species, of which only *H. nanus* occurs in Amazonia. *Holochilus nanus* is a large rat (usually ≥100 g), and it superficially resembles other semiaquatic cricetines by having small ears (not reaching the eye when laid forward) and partially webbed hind feet. However, *H. nanus* is highly distinctive in craniodental morphology (fig. 20). Craniodental traits that distinguish *Holochilus* from *Amphinectomys* and *Nectomys* include a substantially narrower interorbital region; an angular (versus smoothly rounded) anterodorsal margin of the zygomatic plate; much longer and narrower incisive foramina; a narrower, deeply furrowed palate; presence (versus absence) of an alisphenoid strut separating the buccinator-masticatory and accessory oval foramina; and tetralophodont molars with alternating cusps (versus pentalophodont molars with opposite cusps).

Holochilus nanus was previously synonymized with *H. sciureus* Wagner, 1842 (e.g., by Gonçalves et al., 2015), but the molecular clades associated with these names by Prado et al. (2021b) are not sister taxa. According to Prado et al (2021a), *H. nanus* and *H. sciureus* are morphologically diagnosable, and they are allopatric: *H. nanus* being restricted to Amazonia and *H. sciureus* to the Cerrado. However, in side by side comparisons of our Amazonian series with Cerrado specimens (from Goiás), we experienced some difficulty with the craniodental characters

said to distinguish these taxa by Prado et al. (2021a: table 2). Although we apply the name *H. nanus* in the sense recommended by those authors, we are not persuaded that it is consistently diagnosable morphologically from *H. sciureus* based on the specimens we examined.

Our only material of *Holochilus nanus* from the Yavarí-Ucayali interfluve was collected at Orosa by the Olallas in 1926. These old specimens are unaccompanied by external measurements, and the hind feet are too distorted to measure accurately, so only craniodental measurements are available for comparisons with the type and other Amazonian series (table 13). The type is substantially smaller than most of our specimens, but, as noted by Prado et al. (2021a), it is a very young animal. As can be seen, our series overlaps broadly in all craniodental dimensions with Patton et al.'s (2000) specimens from the Rio Juruá, with the exception of zygomatic breadth (ZB), for which those authors reported minimum and maximum values that must be in error (their sample mean is close to ours but outside the reported range of their own data). Gene sequences from the Juruá series were analyzed by D'Elía et al. (2015), who provided the first molecular evidence for the Amazonian clade that Prado et al. (2021b) later recovered by analyzing a genome-wide dataset of single-nucleotide polymorphisms.

Ethnobiology: This species is not known to the Matses, who have no special name for it.
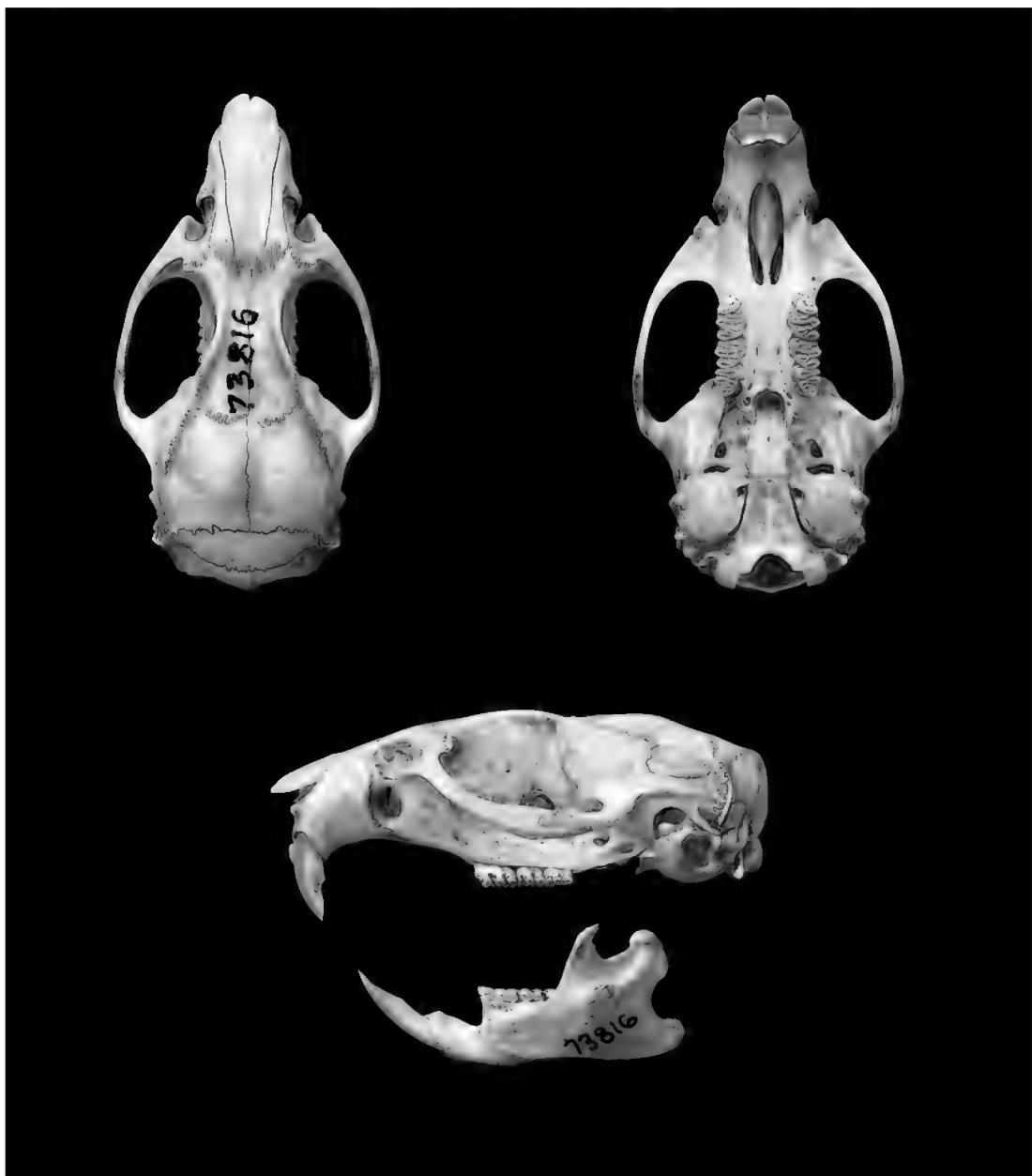
FIG. 20. Dorsal, ventral, and lateral cranial views of *Holochilus nanus* (AMNH 73816). All views about ×1.8.

Matses natural history: No interviews were focused on this species.

Remarks: No ecological information is associated with our material, but Orosa is in the floodplain of the Amazon, which supports a variety of herbaceous nonforest vegetation. We expect that the Olallas trapped this species in situations resembling those in which Patton et al. (2000: 91–92) collected it along the lower Rio Juruá: "in inundated grass patches along the river margins or in small agricultural plots close to the river's edge."

TABLE 13

Measurements (mm) and Weights (g) of *Holochilus nanus*

	BMNH 97.4.1.2[a]	Orosa series[b]	Rio Juruá[c]
HBL	"122"	—	—
LT	"112"	—	155 (126–174) 10
HF	35	—	40 (35–44) 10
Ear	"14"	—	18 (17–19) 10
CIL	30.7	34.3 ± 2.6 (30.7–37.6) 8	35.9 (33.7–37.8) 10
LD	9.5	11.0 ± 1.1 (9.0–12.4) 13	11.3 (10.2–12.4) 10
LM	6.6	7.3 ± 0.2 (6.9–7.7) 13	7.4 (6.7–8.0) 10
BM1	2.0	2.1 ± 0.1 (2.0–2.3) 13	—
LIF	6.8	7.4 ± 0.7 (6.2–8.4) 13	8.0 (7.5–8.6) 10
BIF	2.3	2.6 ± 0.2 (2.2–2.8) 13	—
PBP	2.7	3.0 ± 0.4 (2.2–3.6) 13	—
BZP	4.0	4.4 ± 0.4 (3.5–4.9) 12	4.9 (4.3–5.4) 10
LIB	4.6	4.8 ± 0.2 (4.5–5.2) 13	4.9 (4.4–5.2) 10
ZB[d]	18.7	20.5 ± 1.0 (18.3–21.7) 11	21.0 ("29.2–33.0") 10
LR	—	12.3 ± 0.9 (10.7–13.8) 12	—
Weight	—	—	163 ± 21 (142–181) 4

[a] The holotype, from Marajó Island (Pará, Brazil). Measurements in scare quotes were not taken by the American method.

[b] The mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size for measurements of AMNH 73816–73828.

[c] The mean, the observed range (in parentheses), and the sample size for measurements taken by Patton et al. (2000: table 21), who did not tabulate standard deviations, and who used the following abbreviations that differ from ours: IOC (for LIB), D (for LD), MTRL (for LM), IFL (for LIF), and ZPL (for BZP). We obtained the weight data (not tabulated by Patton et al. 2000 from field notes archived at the MVZ.

[d] Note that the observed range for the Juruá series cannot be correct (see text).

Hylaeamys Weksler et al., 2006

Members of the genus *Hylaeamys*—formerly classified in *Oryzomys* (see Weksler et al., 2006)—are among the most commonly trapped cricetids in cis-Andean lowland rainforests (Percequillo, 2015b). Two species, *H. perenensis* and *H. yunganus*, are sympatric throughout western Amazonia, including the Yavarí-Ucayali interfluve. Unfortunately, these species are not consistently distinguishable in the field because only dental features are diagnostic. Therefore, unvouchered records are unreliable, and even specimens with heavily worn teeth cannot be confidently identified without DNA sequence data.

Capture data summarized below is consistent with previously reported trapping results from other Amazonian research sites (Malcolm, 1991; Patton et al., 2000; Voss et al., 2001; Hice and Velazco, 2012) in suggesting that species of *Hylaeamys* are exclusively terrestrial.

Hylaeamys perenensis (Allen, 1901)

Figures 19B, 19E

Voucher material (*N* = 33): El Chino (UF 30508, 30509), Jenaro Herrera (MUSM 5450 [not seen], 16006–16010 [not seen]), Nuevo San Juan (AMNH 268261, 272688, 272713, 272718, 272826, 273065; MUSM 13326–13331, 15343–

15345), Orosa (AMNH 73829–73832, 74095–74097), San Pedro (UF 30517–30519). Additional material that we have not examined was reported from Jenaro Herrera by Pavlinov (1994) and from Quebrada Betilia by Medina et al. (2015).

UNVOUCHERED OBSERVATIONS: None.

IDENTIFICATION: *Hylaeamys perenensis* (formerly *Oryzomys perenensis*; Weksler et al., 2006) is a widespread western Amazonian species based on a type from Junín department, Peru. The name *perenensis* was treated as a junior subjective synonym of *megacephalus* Fischer, 1814, by Musser et al. (1998), but *H. perenensis* and *H. megacephalus* are apparently not sister taxa (Patton et al., 2000; Bonvicino and Moreira, 2001), and both are now treated as valid species based on molecular sequence divergence, karyotypes, and morphology (Percequillo, 2015b). We follow the current taxonomy uncritically and have not attempted to evaluate the craniodental characters alleged to distinguish these very similar allopatric taxa.

Throughout western Amazonia *Hylaeamys perenensis* occurs sympatrically with another congener, *H. yunganus* (Thomas, 1902). Although these species are externally similar and cannot be consistently distinguished in the field, many specimens of *H. yunganus* lack a hypothenar pad on the hind foot (Musser et al., 1998: fig. 17), whereas a hypothenar pad is consistently present on the hind foot of *H. perenensis*. In effect, a specimen lacking a hypothenar pad is probably *H. yunganus*, but a specimen that has a hypothenar pad cannot be identified as either species. Fortunately, collected voucher material can be readily identified by dental characters (Musser et al., 1998)—except for those with heavily worn molars that lack diagnostic occlusal details. Specimens of *H. perenensis* and *H. yunganus* identified by dental criteria have broadly overlapping measurements (table 11), although some univariate differences are statistically significant (tests not shown).

ETHNOBIOLOGY: This species is not known to the Matses, who have no special name for it.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: Of 13 specimens of *Hylaeamys perenensis* accompanied by ecological data from our region, 5 were taken in primary upland forest, 1 was taken in primary floodplain (seasonally inundated) forest, 3 were taken in swidden agricultural fields, and 4 were taken in secondary vegetation; all specimens were trapped on the ground.

Hylaeamys yunganus (Thomas, 1902)

Figures 19C, 19F

VOUCHER MATERIAL (*N* = 12): El Chino (UF 30540–30542), Nuevo San Juan (MUSM 11221, 13332), San Pedro (UF 30483, 30503, 30526, 30528, 30535, 30543, 30545). Additional material that we have not seen was reported by Pavlinov (1994) from Jenaro Herrera.

UNVOUCHERED OBSERVATIONS: None.

IDENTIFICATION: *Hylaeamys yunganus* (formerly *Oryzomys yunganus*; Weksler et al., 2006) is another widespread species; as currently recognized, it ranges throughout Amazonia from the Atlantic coast to the base of the Andes (Musser et al., 1998; Percequillo, 2015b). As noted by Musser et al. (1998) and Voss et al. (2001), this species exhibits substantial geographic variation in size, with eastern Amazonian specimens averaging smaller than western Amazonian specimens in most external and craniodental dimensions. Crown length of the molar toothrow (LM), for example, is 4.4 ± 0.1 mm in a series from French Guiana (Voss et al., 2001: table 34) versus 4.8 ± 0.1 mm in our series from the Yavarí-Ucayali interfluve (table 11). Nevertheless, other (size-independent) morphological differences between eastern and western Amazonian populations are not apparent, nor do eastern and western Amazonian cytochrome *b* sequences form reciprocally monophyletic haplogroups (Patton et al., 2000: fig. 97), so there is currently no compelling evidence for recognizing additional taxa in the Yunganus Group (sensu Musser et al., 1998).

TABLE 14

Morphological Comparisons between *Neacomys* and *Scolomys*

	Neacomys	*Scolomys*
Tail ratio (LT/HBL)	≥1.0	<1.0
Number of mammae[a]	eight (pectoral pair present)	six (pectoral pair absent)
Zygomatic notches	deep	shallow
Incisive foramina	subparallel	much wider posteriorly than anteriorly
Sphenopalatine vacuities	present	absent
Carotid circulation[b]	pattern 1 or pattern 2	pattern 3
Upper incisors	strongly opisthodont	orthodont or proodont
Capsular process[c]	well developed	indistinct

[a] See Voss and Carleton (1993: fig. 8) for mammary nomenclature.
[b] See Voss (1988: 296–298) for definitions of alternative carotid arterial patterns.
[c] Of the lower incisor alveolus (on the lateral surface of the mandible).

ETHNOBIOLOGY: This species is not known to the Matses, who have no special name for it.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: Ecological information from our region is only available for two specimens of *Hylaeamys yunganus*, both of which were trapped in hollow logs in a palm swamp (*aguajal*). Our data are ecologically inconclusive, but elsewhere in western Amazonia this species is said to be more abundant in upland forest than in floodplain habitats (Patton et al., 2000).

Neacomys Thomas, 1900

Species of *Neacomys* (commonly known as spiny mice) are small cricetids with spiny, reddish-brown dorsal pelage; self-whitish or -buffy underparts; eight mammae; and tails that are about as long as the combined length of head and body. Skulls of *Neacomys* have beaded and anteriorly convergent supraorbital margins; long, narrow, subparallel incisive foramina; and sphenopalatine vacuities in the roof of the mesopterygoid fossa. The carotid circulation is either pattern 1 or pattern 2 (Voss, 1988), the upper incisors are strongly opisthodont, and the capsular process of the lower incisor alveolus is well developed. Species of *Scolomys*—the only

other spiny cricetids in western Amazonia—are easily distinguished from *Neacomys* by conspicuous external and craniodental differences (table 14). *Neacomys* has been the focus of much recent systematic research (e.g., Hurtado and Pacheco, 2017; Sánchez-Vendizú et al., 2018; Semedo et al., 2020, 2021; Brito et al., 2021), with results that have substantially revised the species-level taxonomy previously summarized by Weksler and Bonvicino (2015a). Specimens that we examined from the Yavarí-Ucayali interfluvium can be assigned to two species, but a third can also be expected to occur in our region (appendix 2).

Capture data summarized below is consistent with previously reported trapping results from other Amazonian research sites (e.g., Patton et al., 2000; Voss et al., 2001; Hice and Velazco, 2012) in suggesting that species of *Neacomys* are almost exclusively terrestrial.

Neacomys aletheia Semedo et al., 2021

Figure 21A, 21D

VOUCHER MATERIAL (*N* = 17): Jenaro Herrera (AMNH 276724; MUSM 5457, 15993–15995, 23812, 23813), Nuevo San Juan (AMNH 272867, 272869, 273053; MUSM 13309, 13311–13314,
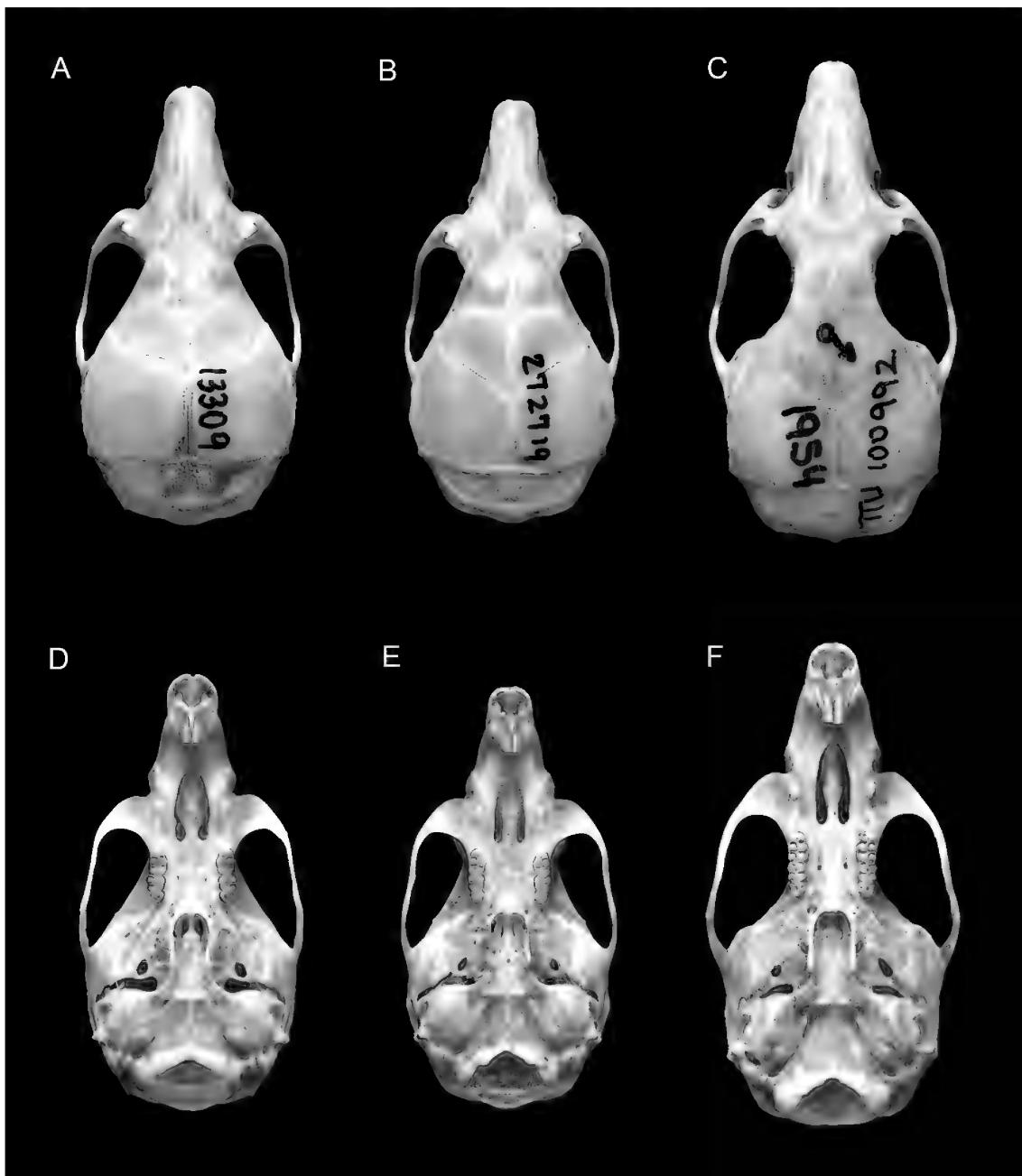
FIG. 21. Dorsal and ventral cranial views of three small oryzomyines: *Neacomys aletheia* (**A**, **D**; MUSM 13309), *N. musseri* (**B**, **E**; AMNH 272719), and *Oligoryzomys microtis* (**C**, **F**; TTU 100992). The skull of *O. microtis* is not from the Yavarí-Ucayali interfluve. Note the shallower zygomatic notches and beaded supraorbital margins in both *Neacomys* species by comparison with the deeper zygomatic notches and squared supraorbital margins in *O. microtis*. All views about ×3.0.

15330, 15331). Additional material originally reported as *Neacomys minutus* by Medina et al. (2015) from Quebrada Betilia and Quebrada Pantaleón was subsequently identified as *N. aletheia* by Sánchez-Vendizú et al. (2021).

UNVOUCHERED OBSERVATIONS: None.

IDENTIFICATION: *Neacomys aletheia* is one of two distinctively small (<20 g) congeneric species that occur sympatrically in the Yavarí-Ucayali interfluve. The other small species in our region, *N. musseri*, is so similar to *N. aletheia* in size and pelage coloration that these species are perhaps externally indistinguishable, and our series likewise overlap in all measured craniodental dimensions (table 15). Apparently, the only morphological character by which *N. aletheia* and *N. musseri* can be unambiguously distinguished concerns the carotid circulation. Whereas *N. aletheia* retains the supraorbital branch of the stapedial artery—which leaves a translucent groove along the inner surfaces of the squamosal and alisphenoid bones and exits the skull via the sphenofrontal foramen (pattern 1 of Voss, 1988: 297–298)—*N. musseri* lacks the supraorbital branch and both of its osteological markers (pattern 2 of Voss, 1988). *Neacomys aletheia* was previously known as the "upriver clade" of *N. minutus* by Patton et al. (2000), who documented its substantial molecular and karyotypic divergence from *N. musseri*.

Phylogenetic analyses of cytochrome *b* sequences obtained from our voucher specimens confirm their identity with the "upriver clade" of *Neacomys minutus* (sensu Patton et al., 2000) and with the species subsequently named as *N. aletheia*. Those analyses (Sánchez-Vendizú et al., 2018; Semedo et al., 2021) additionally suggest that the sister taxon of *N. aletheia* is *N. macedoruizi*, a species that occurs on the north bank of the Amazon, rather than with *N. minutus* sensu stricto (the "downriver clade" of Patton et al., 2000). Morphological, molecular, and karyotypic comparisons of *N. aletheia* (as the "upriver clade" of *N. minutus*) and *N. macedoruizi* were summarized and discussed by Sánchez-Vendizú et al. (2018). Measurements of

our specimens from the Yavarí-Ucayali interfluve are indistinguishable from those of the type series of *N. aletheia* from the Rio Juruá in western Brazil (table 15).

ETHNOBIOLOGY: This species is not known to the Matses, who have no special name for it.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: Thirteen specimens of *Neacomys aletheia* are accompanied by habitat information from our region. Of these, seven were taken in primary upland (well-drained) forest, one was taken in swampy primary forest, one was taken in primary forest of unspecified type, three were taken in secondary vegetation (abandoned swiddens), and one was taken in an active swidden. Ten specimens were trapped on the ground, but three were taken on elevated substrates near ground level (lianas or fallen branches). Most specimens were captured in Sherman traps, but three were taken in pitfalls, two were caught by hand, and one was taken in a deadfall set for *Proechimys* (see below). Two specimens accompanied by microhabitat descriptions were both taken in open hilltop primary forest, one under sparse leafy cover and the other beneath a tangle of fallen branches and dead palm fronds.

Neacomys musseri Patton et al., 2000

Figure 21B, 21E

VOUCHER MATERIAL (*N* = 6): Nuevo San Juan (AMNH 272676, 272687, 272712, 272719; MUSM 13308, 13310).

UNVOUCHERED OBSERVATIONS: None.

IDENTIFICATION: As discussed in the preceding account, the only consistently diagnostic morphological difference between *Neacomys musseri* and sympatric *N. aletheia* concerns the carotid arterial circulation. Apparently, these species are known to occur sympatrically only at Nuevo San Juan.

Neacomys musseri was originally described from 14 specimens collected at two geographically distant localities (>500 km apart): the type

TABLE 15

External and Craniodental Measurements (mm) and Weights (g) of Two Species of *Neacomys*

| | *N. aletheia* | | *N. musseri* | | | |
| | | | Yavarí-Ucayali | | | |
	Yavarí-Ucayali[a]	Type series[b]	AMNH 272687	AMNH 272719	MUSM 13310	SE Peru[c]
HBL	75 ± 3 (71–79) 7	73 ± 4 (67–79) 4	75	—	—	74 ± 3 (70–79) 8
LT	85 ± 5 (78–91) 7	82 ± 2 (80–84) 4	80	—	—	83 ± 5 (77–90) 8
HF	21 ± 0 (20–21) 10	20 ± 1 (19–22) 4	20	20	20	22 ± 0 (22–23) 9
Ear	14 ± 1 (13–14) 8	12 ± 1 (12–13) 4	13	13	—	13 ± 1 (13–15) 9
CIL	18.1 ± 0.4 (17.3–18.5) 14	18.2 ± 0.5 (17.7–18.8) 5	17.2	17.8	17.2	18.9 ± 0.3 (18.5–19.5) 9
LD	5.2 ± 0.2 (4.8–5.5) 14	5.3 ± 0.1 (5.2–5.4) 5	5.0	5.1	5.0	5.5 ± 0.2 (5.2–5.8) 9
LM	2.6 ± 0.1 (2.5–2.7) 16	2.6 ± 0.1 (2.5–2.7) 5	2.5	2.5	2.4	2.7 ± 0.1 (2.6–2.9) 9
BM1	0.8 ± 0.0 (0.7–0.9) 16	0.8 ± 0.0 (0.8–0.8) 5	0.8	0.8	0.8	—
LIF	3.0 ± 0.1 (2.8–3.2) 14	2.8 ± 0.1 (2.7–2.9) 5	2.5	3.0	2.8	3.1 ± 0.1 (2.8–3.3) 9
BIF	1.4 ± 0.1 (1.2–1.7) 14	1.4 ± 0.1 (1.3–1.6) 5	1.3	1.4	1.4	—
BPB	2.2 ± 0.2 (1.9–2.4) 14	—	2.2	2.2	2.1	—
BZP	1.8 ± 0.1 (1.5–2.0) 14	1.8 ± 0.2 (1.7–2.0) 5	1.7	1.8	1.5	—
LIB	4.2 ± 0.2 (4.0–4.6) 14	4.3 ± 0.2 (4.0–4.5) 5	4.5	4.6	4.4	4.3 ± 0.2 (4.0–4.5) 9
ZB	10.6 ± 0.4 (9.6–11.2) 14	10.8 ± 0.3 (10.5–11.2) 5	10.3	10.3	9.9	11.4 ± 0.3 (11.0–11.8) 8
LR	6.5 ± 0.2 (6.2–7.0) 14	—	6.1	6.4	6.2	—
Weight	14 ± 2 (12–17) 10	13 ± 1 (11–15) 4	14	12	10	—

[a] The mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size for measurements of the following series: AMNH 272867. 272869, 273053, 276724; MUSM 5457, 13309, 13311–13314, 15330, 15331, 23812, 23813, 15993–15994.

[b] From the Rio Juruá in western Brazil (Amazonas). Measurement data from Semedo et al. (2021: table 2).

[c] The type series plus topotypes, all from Cusco department. The mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size for measurements of the following series (data courtesy of J.L. Patton): MVZ 171483–171489; UMMZ 160542, 160543.

series from 72 km NE of Paucartambo in Cusco department, Peru, and a single specimen from the upper Rio Juruá in Amazonas state, Brazil (Patton et al., 2000: 98). Measurements of specimens from the Yavarí-Ucayali interfluve are consistently smaller in several craniodental dimensions than the SE Peruvian type series (table 15), but cytochrome *b* sequence analyses (Sánchez-Vendizú et al., 2018) support the application of this name to our material.

ETHNOBIOLOGY: This species is not known to the Matses, who have no special name for it.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: Six specimens of *Neacomys musseri* are accompanied by habitat information from our region. All were taken on the ground in Sherman traps in sheltered microhabitats (under fallen trunks, inside hollow logs, or beneath leafy cover) in well-drained primary forest. Three of these were taken in valley-bottom forest, and three on hillsides or on a hillcrest.

Nectomys Peters, 1861

Species of *Nectomys*, commonly known as water rats, are distinctively large (>150 g) amphibious cricetids that occur in or near

streams and rivers throughout much of tropical and subtropical South America below about 2500 m. Five species are currently recognized (Bonvicino and Weksler, 2015), of which two occur in the Yavarí-Ucayali interfluve. Water rats have glossy-brownish or -blackish-brown dorsal fur; gray-based buffy ventral fur; small ears (not reaching the eye when laid forward); long, macroscopically naked, unicolored (all dark) tails; and large hindfeet with small interdigital webs (not extending distally beyond the ends of the first phalanges), naked claws (not concealed by ungual tufts), and visibly scaly soles. Water rat skulls have deep zygomatic notches; anteriorly convergent interorbital regions with well-developed supraorbital beads; long palates; well-developed, complex, and deeply recessed posterolateral palatal pits; and derived carotid circulations (pattern 3 of Voss, 1988). There is usually a notch in the posterolateral margin of the squamosal that is homologous with the subsquamosal fenestra of other Neotropical cricetids, but the fenestra itself is not patent. The molars are higher crowned than those of most other oryzomyines, pentalophodont (with well-developed mesolophs and mesolophids), and lophodont (with interpenetrating lingual and labial flexi). Morphological comparisons with the closely related genus *Amphinectomys* have already been discussed in the account for *A. savamis* (above) with the most conspicuous contrasts summarized in table 9.

ETHNOBIOLOGY: The Matses do not recognize more than a single species of water rat in their tribal territory, but the specimens we collected in the vicinity of Nuevo San Juan are all *Nectomys apicalis*, so our ethnographic information is summarized in the following account.

Nectomys apicalis Peters, 1861

Figures 18B, 18E, 22A, 23A, 24A

VOUCHER MATERIAL (*N* = 12): Nuevo San Juan (AMNH 268255, 268256, 273135; MUSM 11203–11207, 15332), San Pedro (MUSM 22344, 22345; UF 30787).

UNVOUCHERED OBSERVATIONS: Field identifications of this species cannot be accepted as valid without supporting voucher material.

OTHER SPECIMENS EXAMINED[15] (*N* = 136): **Brazil**—*Amazonas*, Barro Vermelho (MVZ 190374*), Jainu (MVZ 190373*). **Ecuador**—*Orellana*, 42 km S Pompeya Sur (ROM 104495, 106067, 106081); *Sucumbios*, Limoncocha (USNM 513585*), *Zamora-Chinchipe*, Los Encuentros (USNM 513584*). **Peru**—*Amazonas*, Huampami (MVZ 153539*, 153568, 153569, 155018, 155019*–155022, 155024–155029), La Poza (MVZ 157813–157827), San Antonio (MVZ 153534*), 46 km SE Bagua Grande (LSUMZ 19296); *Ayacucho*, Hacienda Luisiana (LSUMZ 16711*), San José (LSUMZ 16715*), Santa Rosa (LSUMZ 15694); *Cusco*, Hacienda Cadena (FMNH 65687–65694), Hacienda Villa Carmen (FMNH 84290–84295), Kiteni (USNM 19297), Ocobamba (USNM 86917, 86918), Río Comberciato (USNM 194830), San Fernando (USNM 194832, 194833, 194835–194837), San Pedro (FMNH 172263–172265), Santa Ana (USNM 194907, 194909, 194910, 194912–194915), Uvini (USNM 194831), 40 km E Quincemil (USNM 19298), 15.9 km SW Pilcopata (FMNH 175091); *Huánuco*, Hacienda Vista Alegre (FMNH 24131), Tingo Maria (FMNH 46101, 46102); *Junín*, Perené (AMNH 63857), Río Tulumayo (USNM 507262*); *Loreto*, Boca Río Curaray (AMNH 71909–71911, 71913, 71915–71920), Boca Río Peruaté (FMNH 88912), 25 km S Iquitos (TTU 98642, 98994, 100883, 124939, 124940), Puerto Indiana (AMNH 73351, 73352), San Jacinto (KU 158188, 158189); *Madre de Dios*, confluence of Río La Torre with Río Tambopata (LSUMZ 24593), Hacienda Amazonía (FMNH 139832, 139833, 139835), 2.75 km E Shintuya (FMNH 170593), Puerto Maldonado (KU 144301, USNM 390136); *Pasco*, San Ramón (AMNH 213534); *Puno*,

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[15] Specimens marked with asterisks (*) are those karyotyped by Gardner and Patton (1976), Patton et al. (2000), or Bonvicino and Gardner (2001).
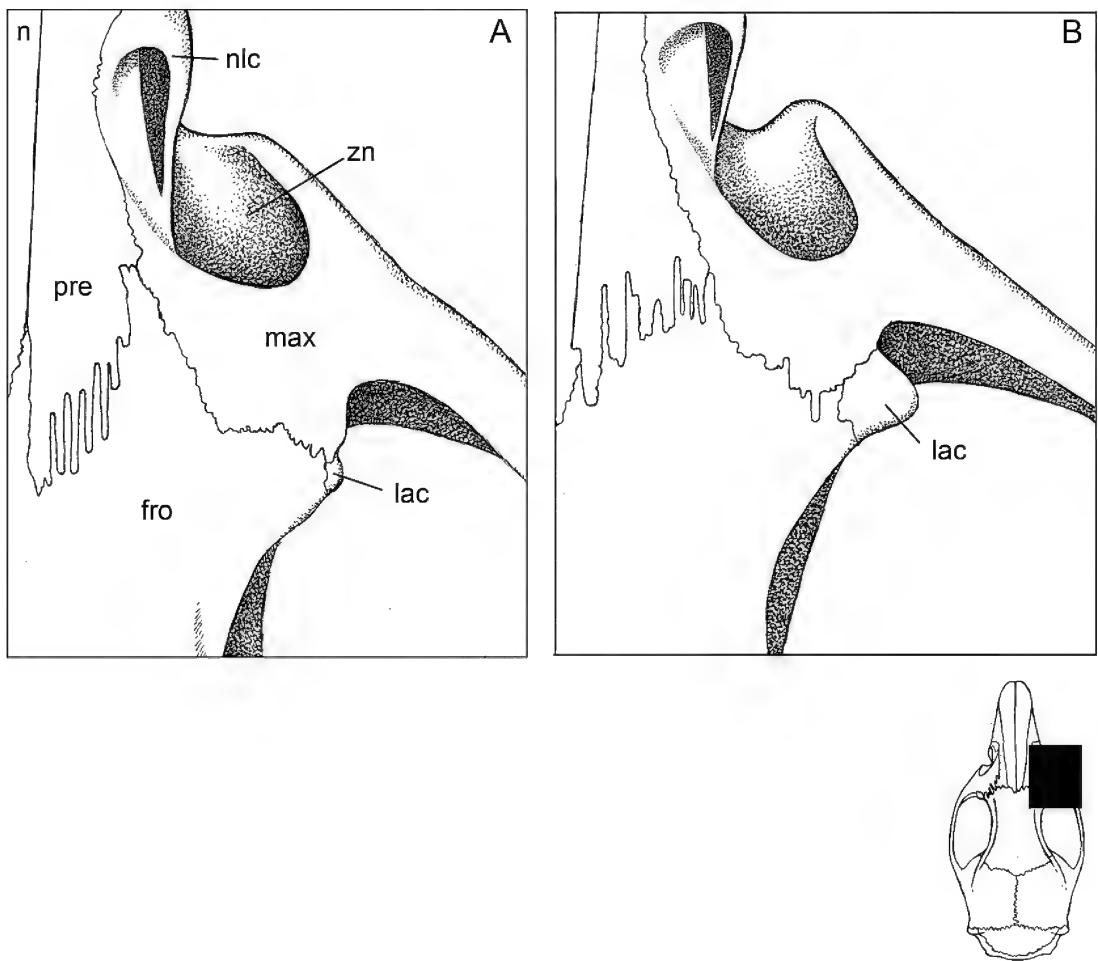
FIG. 22. Dorsal views of anterior orbital region of *Nectomys apicalis* (**A**, AMNH 71915) and *N. rattus* (**B**, AMNH 231154) illustrating species difference in lacrimal size. Abbreviations: **fro**, frontal; **lac**, lacrimal; **max**, maxillary; **n**, nasal; **nlc**, nasolacrimal capsule; **pre**, premaxillary; **zn**, zygomatic notch.

Carabaya (USNM 137520, 172961), San Juan (FMNH 78378–78383), Santo Domingo (= "Inca Mines"; AMNH 15801, 16057; FMNH 18201, 29452); *Ucayali*, Balta (LSUMZ 12321, 12324, 12326–12329, 14377, 16708; MVZ 136639–136641*), Lagarto (AMNH 76512, 76520), Santa Rosa (AMNH 76057).

IDENTIFICATION: Peruvian specimens of *Nectomys* can be sorted into two taxa that we identify as *Nectomys apicalis* and *N. rattus* based on qualitative and morphometric trait differences. We have not examined the type material of either

species (in Berlin and Vienna, respectively), but we provisionally accept the application of these names as recommended by Bonvicino and Weksler (2015). As currently understood, *Nectomys apicalis* is a western Amazonian taxon characterized by diploid counts of 38–42 chromosomes, whereas *N. rattus* is a widespread (pan-Amazonian) species with $2n$ = 52–56 chromosomes. According to Patton et al. (2000), these karyotypes can be associated with different cranial phenotypes: specimens with $2n$ = 38–42 have interparietals that are deep (anteroposterior
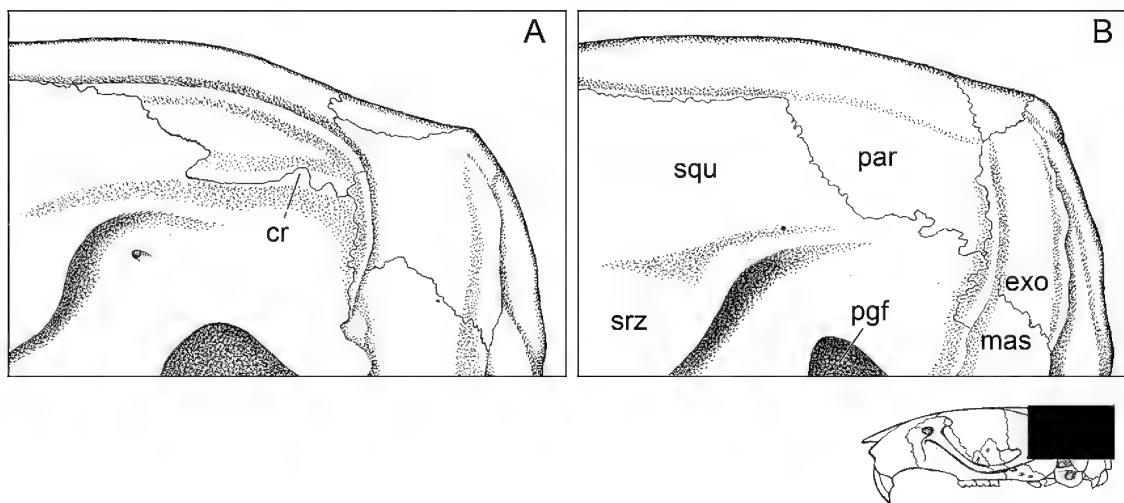
FIG. 23. Dorsolateral braincase of *Nectomys apicalis* (**A**, AMNH 273135) and *N. rattus* (**B**, AMNH 231154) illustrating species difference in presence or absence of a low crista (**cr**) along the parietal-squamosal suture. Other abbreviations: **exo**, exoccipital; **mas**, mastoid exposure of petrosal; **par**, parietal; **pgf**, postglenoid foramen; **srz**, squamosal root of zygomatic arch; **squ**, squamosal.

dimension) in proportion to their width (transverse dimension), whereas specimens with $2n = 52–56$ have interparietals that are proportionately shallower. Although Patton et al. (2000) suggested that the ratio of interparietal depth (IPD) to interparietal width (IPW) could be used as a diagnostic criterion, our measurements of karyotyped specimens—those marked with asterisks in lists of examined material (above and below)—resulted in narrowly overlapping values of this ratio (IPD/IPW). Fortunately, other morphological traits allow confident identification of these species (table 16).

Several qualitative craniodental characters described by Chiquito (2015) are correlated with interparietal shape and, in combination, can be used to sort western Amazonian specimens into two distinct groups: (1) The dorsal exposure of the lacrimal bone at the anteromedial corner of the orbit is usually small in specimens with deep/narrow interparietals (fig. 22A), but the lacrimal tends to be conspicuously larger in specimens with shallow/wide interparietals (fig. 22B). (2) The suture between the parietal and the squamosal on the posterolateral braincase—above and behind the squa-

mosal root of the zygomatic arch—is produced as a low crest in most specimens with deep/narrow interparietals (fig. 23A), but a sutural crest is absent in most specimens with shallow/wide interparietals (fig. 23B). (3) The incisive foramina in specimens with deep/narrow interparietals are parallel sided or taper anteriorly without interruption, and the median septum that divides the left and right foramina is uniformly narrow (fig. 24A); by contrast, in specimens with shallow/wide interparietals, the incisive foramina are laterally constricted anterior to the premaxillary/maxillary suture, and the median septum is conspicuously flattened or dimpled at a point corresponding to the lateral constriction (fig. 24B).

Adult specimens[16] of *Nectomys* from western Amazonia with deep/narrow interparietals, small lacrimals, crested parietal/squamosal sutures, and unconstricted incisive foramina include six with $2n = 38–42$ chromosomes (LSUMZ 16711, 16715; MVZ 155019, 190373, 190374; USNM 513585), whereas western Amazonian adults

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[16] Some of these traits are not consistently developed in juveniles.
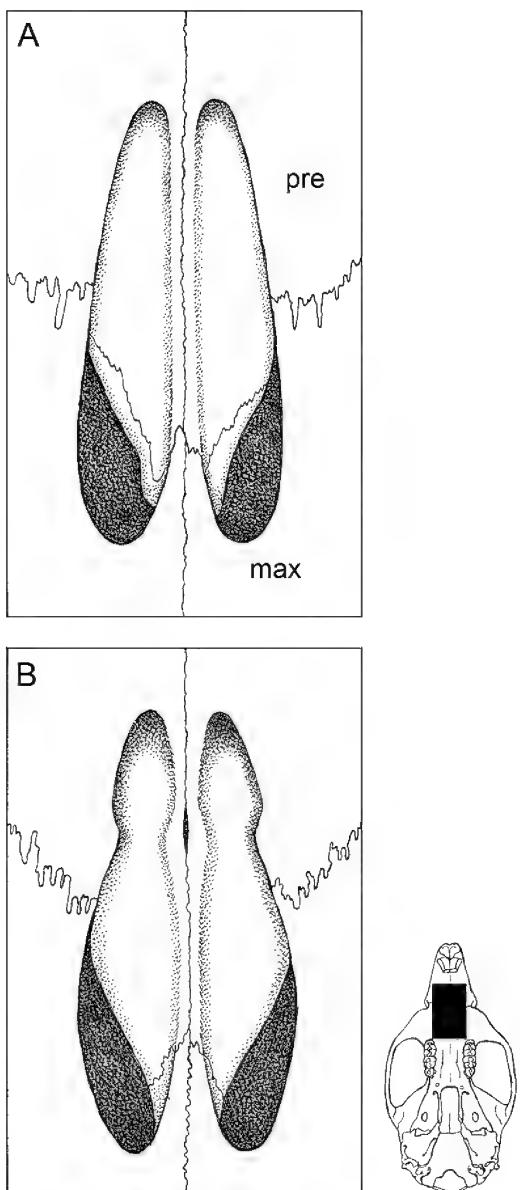
FIG. 24. Incisive foramina of *Nectomys apicalis* (**A**, MUSM 11204) and *N. rattus* (**B**, AMNH 231160) illustrating species difference in foraminal shape (see text). Note the flattened (wider) region of the septum at the point of lateral constriction in *N. rattus*. Abbreviations: **max**, maxillary bone; **pre**, premaxillary.

with shallow/wide interparietals, large lacrimals, uncrested parietal/squamosal sutures, and constricted incisive foramina include three with $2n$ = 52 chromosomes (LSUMZ 14372–14374). Both phenotypes occur in Loreto department, where they are also morphometrically divergent, especially in molar toothrow length (table 17). Unfortunately, we have not discovered any external character by which these species might be confidently identified in the field.

Peters' (1861) illustration of the holotype skull of *Nectomys apicalis* is consistent with the application of this name to the western Amazonian species with deep/wide interparietals, small lacrimals, and unconstricted incisive foramina (the morphology of the posterolateral braincase is not sufficiently resolved in Peter's figure to confirm the presence of a parietal-squamosal crest). As noted by Hershkovitz (1944: 25–26), the type was purchased at Guayaquil (presumably from a dealer in natural history curiosa), but it was almost certainly collected in eastern Ecuador. According to Chiquito's (2015) revision, *N. apicalis* occurs in eastern Colombia, eastern Ecuador, eastern Peru, and eastern Bolivia. We additionally recognize Patton et al.'s (2000) material from the Rio Juruá in western Brazil as *N. apicalis*, whereas Chiquito refers their Juruá material to an unnamed taxon ("*Nectomys* sp. B") that also includes two MVZ specimens from Balta (in Ucayali department, Peru). Molecular sequence data would be helpful in resolving inconsistencies between Chiquito's restricted usage of *N. apicalis* and our more inclusive application of this name.

ETHNOBIOLOGY: The Matses name for the water rat is maka tanun ("gray rat"). No subtypes are recognized by the Matses, and they have no synonyms for this species. The water rat is a very minor game animal for the Matses. It is sometimes killed in deadfall traps baited with manioc. While some Matses eat them, others do not, and those who do eat them discard any that are infested with botfly larvae. Water rats are pests that feed on crops in swiddens surrounded by forest and on crops planted next to houses in

TABLE 16

Morphological Comparisons between *Nectomys apicalis* and *N. rattus* from Loreto Department, Peru

	N. apicalis	*N. rattus*
Interparietal ratio (IPD/IPW)[a]	0.45 ± 0.06 (0.38–0.61) 23	0.34 ± 0.05 (0.23–0.40) 14
Incisive foramen constriction	usually absent	usually present
Dorsal exposure of lacrimal bone	usually small	usually large
Crista along parietal-squamosal suture	usually present	usually absent

[a] See text. Tabulated statistics are the sample mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size.

clearings. They also frequently prey on poultry (hatchling chickens and Muscovy ducks). They are killed with a stick if they are found near poultry sheds.

MATSES NATURAL HISTORY: Water rats are similar in size and shape to spiny rats (*Proechimys* spp.), but they have grayish ventral fur, no spines in the dorsal fur, and a longer snout.

They live in the forest and in grassy areas near Matses houses. They are abundant in swampy areas, both in the forest and near Matses houses, and at the edges of streams and rivers.

Water rats makes their nests in hollow logs, in piles of brush, at the bases of tree stumps, in the crowns of underlined pinchuk palms (*Astrocaryum murumuru*) that have not yet grown a stem, or at the bases of plantain plants in swiddens where there are many daughter plants growing from the base of the parent tree. In all these situations, the nest is made by bringing together many dry leaves (dead plantain leaves in the latter case). They also make nests of dry grass among clumps of grass.

The water rat is nocturnal.

Water rats often have large botfly larvae.

Water rats eat dicot tree fruits. In swiddens they eat manioc tubers, plantain fruits, papayas, cush-cush yams, malanga corms, and sweet potatoes.

REMARKS: Capture data are available from 12 specimens positively identified as *Nectomys apicalis* from the Yavarí-Ucayali interfluve, all of which were collected at Nuevo San Juan. Of these, 7 (58%) were taken by children in deadfall traps set in swiddens for *Proechimys* (see below), and another was captured by hand in a swidden at

night. Three others were taken in deadfalls set in secondary growth, and one was killed in the daytime by a Matses man while clearing weeds around the village. Most of the swiddens in which *N. apicalis* were trapped were close to the Río Gálvez, but one capture was made in a swidden that was >100 m from the nearest stream.

Although none of our vouchers from Nuevo San Juan were taken in natural habitats, Valqui (2001) reported that specimens of *Nectomys* from San Pedro (three of which we identified as *N. apicalis*; see above) were trapped "almost exclusively in streambeds." Patton et al.'s (2000) specimens were mostly trapped along streams in both primary and secondary forest, although some were taken in nearby garden plots. Matses observations that these large rats prey on chickens as well as consuming garden fruits and tubers are consistent with previous suggestions that species of *Nectomys* are omnivorous (Ernest, 1986; Ernest and Mares, 1986).

Nectomys rattus (Pelzeln, 1883)

Figures 18C, 18F, 22B, 23B, 24B

VOUCHER MATERIAL (*N* = 6): El Chino (MUSM 22342, 22343; UF 30467, 30468), Jenaro Herrera (MUSM 15998, 15999).

UNVOUCHERED OBSERVATIONS: None (field identifications of this species cannot be accepted as valid without supporting voucher material).

OTHER SPECIMENS EXAMINED (*N* = 49): **Peru**—*Loreto*, Lagunas (FMNH 19648, 19649; USNM 274566), Mouth of Potro River (AMNH

TABLE 17

**External and Craniodental Measurements (mm) and Weights (g) of *Nectomys apicalis*
and *N. rattus* from Loreto Department, Peru**

	N. apicalis[a]	*N. rattus*[b]	Difference[e]
HBL	213 ± 24 (178–241) 12	189 ± 14 (176–220) 8[c]	—
LT	205 ± 17 (176–240) 12	190 ± 15 (170–210) 8[c]	—
HF	51 ± 2 (47–55) 12	50 ± 2 (46–53) 10[d]	n.s.
Ear	22 ± 1 (20–25) 12	20 ± 1 (18–22) 5[c]	—
CIL	41.6 ± 2.4 (37.3–45.1) 23	39.2 ± 1.6 (37.6–42.6) 15	*
LD	12.4 ± 1.0 (10.6–14.0) 23	12.1 ± 1.0 (11.2–15.2) 16	n.s.
LM	7.4 ± 0.2 (7.1–7.8) 22	6.7 ± 0.2 (6.2–7.1) 15	**
BM1	2.3 ± 0.1 (2.1–2.4) 23	2.1 ± 0.1 (2.0–2.3) 16	**
LIF	7.2 ± 0.5 (6.5–8.2) 23	7.7 ± 0.6 (7.0–9.2) 17	*
BIF	3.2 ± 0.2 (2.6–3.6) 23	3.4 ± 0.2 (3.1–3.7) 17	*
BPB	4.5 ± 0.5 (3.8–5.2) 23	4.5 ± 0.3 (4.0–4.9) 16	n.s.
BZP	4.8 ± 0.4 (4.0–5.5) 22	4.8 ± 0.4 (4.3–5.6) 17	n.s.
LIB	7.1 ± 0.4 (6.4–8.0) 23	7.2 ± 0.4 (6.5–8.0) 17	n.s.
ZB	24.0 ± 1.5 (21.0–26.1) 20	22.7 ± 0.8 (21.6–24.3) 16	*
LR	14.6 ± 0.9 (12.7–16.2) 23	14.2 ± 1.0 (12.7–17.0) 16	n.s.
Weight	268 ± 70 (160–370) 11	—	—

[a] The mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size for measurements of the following series: AMNH 71909–71911, 71913, 71915–71920, 73351, 73352, 268255, 268256, 273135; FMNH 88912; MUSM 11203–11205; TTU 98642, 98994, 100883, 124939, 124940.

[b] The mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size for measurements of the following series: AMNH 76299–76301, 76458, 76462, 76463, 99263; BMNH 28.5.2.152, 28.5.2.154, 28.5.2.156, 28.5.2.157; FMNH 19644, 19645, 19648, 19649, 46100; USNM 274566.

[c] Summary statistics include measurements recorded by British collectors.

[d] Hind feet measured by British collectors were remeasured by R.S.V.

[e] Results of two-tailed *t*-tests assuming unequal variances (Welch's *t*-tests). We did not test for differences in HBL, LT, and Ear, which were measured differently by British and American collectors. Symbols: * = $p < 0.01$, ** = $p \ll 0.01$, n.s. = not significant ($p \geq 0.05$).

99263), Puerto Arturo (FMNH 19644, 19645), San Jerónimo (BMNH 28.5.2.152–28.5.2.157; FMNH 46100), Sarayacu (AMNH 76299–76301, 76458, 76462, 76463); *Pasco*, Loma Linda (AMNH 213530), Nevatí Mission (AMNH 231167, 231174, 231178, 231179, 231753, 231895, 231896, 239961), Pozuzo (FMNH 24120–24127, 34254, 34255), San Pablo (AMNH 231148, 231151, 231154, 231156, 231159, 231160); *Ucayali*, 59 km SW Pucallpa (USNM 499226), Yarinacocha (LSUMZ 14372–14375).

IDENTIFICATION: *Nectomys rattus* can be distinguished from *N. apicalis* by qualitative and morphometric traits described, illustrated, and tabulated in the preceding species account. The geographic ranges of these species overlap in northern Peru (Loreto, Pasco, and Ucayali departments),[17] but they are not known to be sympatric anywhere. However, Michael Valqui's specimens of *N. rattus* from El Chino were collected only about 5 km from San Pedro—where

[17] Bonvicino and Weksler (2015) included *montanus* Hershkovitz, 1944, in the synonymy of *Nectomys rattus*, which would extend the range of that species to Huánuco, but Chiquito (2015: 154) synonymized *montanus* with *N. apicalis*. All the specimens of water rats from Huánuco examined by Chiquito and by us are examples of *N. apicalis*.

N. apicalis was collected—so it seems probable that these taxa might occur together (but perhaps not syntopically) at some intermediate place or elsewhere in our region.

This is the same species that some authors (e.g., Voss et al., 2001) previously called *Nectomys melanius* (Thomas, 1910) from northeastern Amazonia. Northeastern Amazonian specimens are morphologically indistinguishable from western Amazonian specimens (e.g., exhibiting all the qualitative traits listed for the species in table 16), and they have similar karyotypes ($2n = 52–56$). We have not examined the type of *N. rattus* (an immature specimen collected almost 200 years ago at Marabitanas on the upper Rio Negro), but adult specimens from localities upstream and downstream of the type locality (e.g., USNM 560650, AMNH 79398) support the synonymy of these nominal taxa. Most western Amazonian specimens of *N. rattus* are not accompanied by weight data, but five that we examined for this report weighed 271 ± 86 g.

ETHNOBIOLOGY: This species is not known to occur in Matses territory.

MATSES NATURAL HISTORY: The Matses have no knowledge of this species.

REMARKS: According to Valqui (2001), this species—which he identified as *Nectomys squamipes*—was trapped at El Chino close to streams and oxbow lakes on *restingas* (levees), in tall *várzea*, and in waterlogged stands of spiny palms.

Oecomys Thomas, 1906

Species of *Oecomys* are semiarboreal cricetids that occur throughout the forested Neotropical lowlands from Costa Rica to northern Argentina (Carleton and Musser, 2015). Multiple sympatric species occur in local faunas throughout Amazonia (Voss and Emmons, 1996; Patton at al., 2000; Voss et al., 2001; Hice and Velazco, 2012), which appears to be the center of diversity for this taxonomically challenging genus. Although progress has been made in sorting out the species that occur in eastern Amazonia (Voss et al., 2001; Rocha et al., 2018; Suárez-Villota et al., 2018),

the identification of western Amazonian *Oecomys* remains problematic.

Species of *Oecomys* can be distinguished from members of other oryzomyine genera by the following combination of morphological traits: (1) long mystacial vibrissae (laid back alongside the head, these sensory hairs always extend well beyond the tips of the pinnae); (2) unwebbed hind feet with a long, semiprehensile fifth digit and large, fleshy plantar pads; (3) soft (nonspinous) fur; (4) beaded, ridged, or crested supraorbital margins that are always anteriorly convergent; (5) a zygomatic plate that is variable in width but that never has a spinous dorsal process; (6) a long-wide palate; and (7) pentalophodont, brachydont-bunodont molars that are incipiently lophodont (with shallowly interpenetrating labial and lingual flexi). Species of *Oecomys* are sometimes confused in the field with species in other oryzomyine genera—especially *Euryoryzomys* and *Hylaeamys*—but the morphology of the hind foot (illustrated by Voss et al., 2001: fig. 53) is diagnostic.

Morphological characters that vary among species of *Oecomys* include (inter alia) size; dorsal fur length; ventral fur pattern and coloration; length and density of ungual hairs at the bases of digits II–V of the hind foot; caudal scale size (inversely correlated with scale-row counts per centimeter); presence/absence of a distinct pencil of long hairs on the tail tip; depth of the zygomatic notches on either side of the rostrum; presence/absence of postorbital processes; length of the incisive foramina relative to diastemal length (as quantified by the ratio LIF/LD); presence of a bony strut of the alisphenoid (separating the buccinator-masticatory foramen from the accessory oval foramen); carotid arterial morphology; presence/absence and size of the subsquamosal fenestra; overlap between the tegmen tympani and the posterior edge of the squamosal; and the presence, absence, and size of preputial glands. Although taxonomic variation has sometimes been described in the width and shape of the mesopterygoid fossa, the number and depth of the

posterolateral palatal pits, shape of the zygomatic arches, and details of molar occlusal morphology, substantial individual (intraspecific) variation in all these features makes it difficult to use them for diagnostic purposes.

Karyotypes are also highly variable in the genus, with known diploid numbers ranging from 54 to 90 chromosomes (Sokolov and Malygin, 1994; Patton et al., 2000; Gomes et al., 2016). Unhappily, many specimens of *Oecomys* (including the ones we collected in the Yavarí-Ucayali interfluve) are not accompanied by karyotypic data, so this useful source of taxonomic information is not consistently available.

Sympatric species of *Oecomys* can usually be distinguished morphologically, but diagnostic features are often subtle, and associating local phenotypes with name-bearing material from distant localities is sometimes difficult. To supplement our morphological comparisons, we analyzed cytochrome *b* gene sequences from specimens collected throughout western Amazonia, including new sequence data obtained by us and additional sequences downloaded from GenBank. In total, we analyzed sequence data from 143 specimens of western Amazonian *Oecomys*, of which 17 were collected in the Yavarí-Ucayali interfluve (appendix 3).

Based on maximum-likelihood analysis of these data and our examination of voucher material and other specimens, we recognize a total of eight species in western Amazonia, of which at least five occur in the Yavarí-Ucayali interfluve (fig. 25). Of the five species in our region, two are members of widespread complexes (*O. bicolor*, *O. roberti*), and three are described as new in the following accounts (*O. galvez, O. nanus, O. makampi*). Of the three additional western Amazonian species, one is apparently restricted to the north bank of the Amazon (*O.* "*paricola*" sensu Carleton and Musser, 2015), one is widespread north and south of the Amazon and might eventually be found in our region (*O. superans*), and one is only known from scattered localities along the base of the Andes (*O. osgoodi*, currently treated as a synonym of *O. trinitatis* sensu Car-

leton and Musser, 2015).[18] Average uncorrected pairwise (p) distances among these taxa range from 7.4% to 11.1% (table 18).

Of the five species of *Oecomys* known to occur in our region, three are small and have self-white ventral fur (the hairs entirely white from tips to roots), whereas two others are substantially larger and have gray-based ventral fur. In the following accounts we treat the small species with self-white ventral pelage first.

Oecomys bicolor (Tomes, 1860)

Figures 26A, 26D, 28A

Voucher material (*N* = 22): Jenaro Herrera (MUSM 16000), Nuevo San Juan (AMNH 268257, 268258, 272674, 272710, 272724, 272727, 273064, 273096; MUSM 11208, 11211, 11213, 13315–13319, 15333, 15334), San Pedro (UF 30469), Santa Cecilia (FMNH 87203, 87204). Pavlinov (1994) reported additional specimens from Jenaro Herrera in the ZMMU that we have not seen.

Unvouchered observations: None that can be reliably identified as such given the presence of other externally similar species in our region (see below).

Other specimens examined (*N* = 66): **Brazil**—*Acre*, Igarapé Porongaba on right bank of Rio Juruá (MVZ 200958, 200959), Nova Vida on right bank of Rio Juruá (MVZ 200963), opposite Igarapé Porongaba on left bank of Rio Juruá (MVZ 200882), Sobral on left bank of Rio Juruá (MVZ 200962); *Amazonas*, Barro Vermelho on left bank of Rio Juruá (MVZ 200884, 200964), Colocação Vira Volta on left bank Rio Juruá (MVZ 200956), Igarapé Nova Empresa on left bank of Rio Juruá (MVZ 200966, 200967), Sacado on right bank of Rio Juruá (MVZ 200897); **Ecuador**—*Morona-Santiago* Gualaquiza (BMNH 7.1.1.96 [holotype]); *Orellana*, 35

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[18] Although *Oecomys concolor* was listed as expected in our region by Escobedo-Torres (2015), the known distribution of *O. concolor* is restricted to the Río Negro basin of eastern Colombia, southern Venezuela, and northern Brazil; it is not known to occur in Peru (Carleton and Musser, 2015).
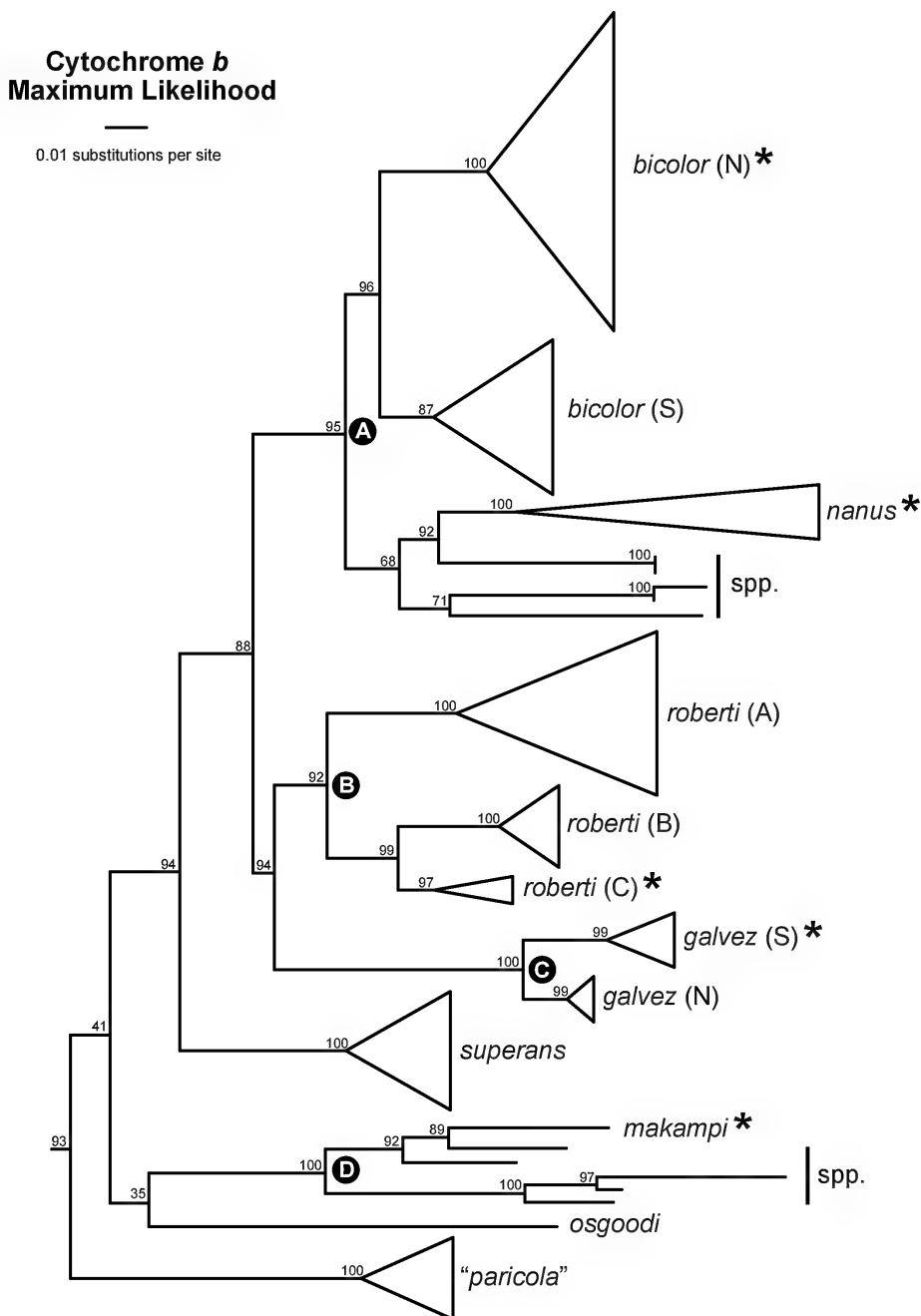
FIG. 25. Maximum-likelihood topology for 143 cytochrome *b* sequences of *Oecomys* from western Amazonia. Species and haplogroups discussed in the text are cartooned as triangles, each with base proportional to number of member sequences and height proportional to genetic diversity. Bootstrap support values are provided above each branch. Bolded uppercase letters (**A–D**) indicate nodes that are fully resolved in subsequent figures. Asterisks (*) indicate taxa that are represented by specimens collected in the Yavarí-Ucayali interfluve. Outgroups (see Materials and Methods) are not shown.

TABLE 18

**Average Percent Uncorrected Cytochrome *b* Sequence Divergence within and among
Western Amazonian Species of *Oecomys***

	bicolor	galvez	makampi	nanus	osgoodi	"paricola"	roberti	superans
bicolor	**3.30**							
galvez	9.44	**2.27**						
makampi	10.02	10.48	—					
nanus	7.79	9.94	9.17	**2.87**				
osgoodi	9.60	10.73	11.07	9.88	—			
"paricola"	10.57	11.00	10.92	10.25	9.81	**1.07**		
roberti	7.51	8.12	10.07	8.68	9.10	10.70	**4.87**	
superans	8.47	8.61	9.38	9.24	9.22	9.50	7.42	**1.88**

km S Pompeya Sur (ROM 105519, 105597, 105660), 38 km S Pompeya Sur (ROM 105329, 118794, 118873), 42 km S and 1 km E Pompeya Sur (ROM 104505, 118884, 118911), Tiputini Biodiversity Station (ROM 106153); *Pastaza*, Canelos (AMNH 67404, 67504), 5 km N Puyo (TTU 84901, 85228). **Peru**—*Amazonas*, vicinity of Huampami on Río Cenepa (MVZ 154988, 154990–154992, 154997, 154999, 155001); *Loreto*, Collpa Salvador (MUSM 17571), Estación Biológica Allpahuayo (TTU 98621, 98766, 98829, 100834), Iquitos (TTU 124943), Km 48 on Iquitos-Nauta Highway (TTU 124945), Km 48.3 on Iquitos-Nauta Highway (TTU124951, 124952, 124954), Km 50 on Iquitos-Nauta Highway (TTU 124950), Km 52 on Iquitos-Nauta Highway (TTU 124947, 124949), Km 60.4 on Iquitos-Nauta Highway (TTU 124942), Nina Rumi (MUSM 45737–45743), Pachacutec (MUSM 43188); *Madre de Dios*, Reserva Cuzco Amazónico (KU 144302, 144304, 144305, 144314, 144322, 144325, 144327); *Ucayali*, Balta on Río Curanja (LSUMZ 12385, 14362–14364).

IDENTIFICATION: This is the only species of *Oecomys* in our region that we can confidently associate with an existing name. Adult specimens of *O. bicolor* (sensu stricto; see below) are small (<40 g) mice with diagnostically short (4–6 mm) dull reddish-brown dorsal pelage. The ventral pelage is immaculately self-white from chin to anus (the individual hairs white to their roots),

without any buffy markings and without conspicuous lateral zones of gray-based hairs; the transition to the reddish-brownish color of the flanks is abrupt, without any intervening lateral line of clear buffy fur. The tail is unicolored (all dark) and relatively short (LT/HBL = 1.07 ± 0.09), and the pencil of apical hairs is also short (≤5 mm). Caudal scale counts (obtained from several fluid-preserved specimens) range from 19 to 24 rows/cm on the proximal third of the tail. Four dissected adult male specimens (AMNH 272710, 272727; MUSM 13318, 15334) had no visible preputial glands.

In dorsal cranial view (fig. 26A) the rostrum is slender, and its base is flanked by very shallow zygomatic notches. In ventral cranial view (fig. 26D) the incisive foramina are long relative to diastemal length (LIF/LD = 0.66 ± 0.02) and relatively narrow (BIF/LIF = 0.46 ± 0.03); they are usually widest near their middle section and taper evenly posteriorly and anteriorly. The upper molar toothrow is consistently less than 4.2 mm. Alisphenoid struts (separating the buccinator-masticatory and accessory oval foramina) are usually absent among the specimens we examined. Subsquamosal fenestrae are always present and patent (fig. 28A), the tegmen tympani seldom contacts the posterior edge of the squamosal, and the mastoid capsules are almost always fenestrated. The carotid circulation is complete, with a well-
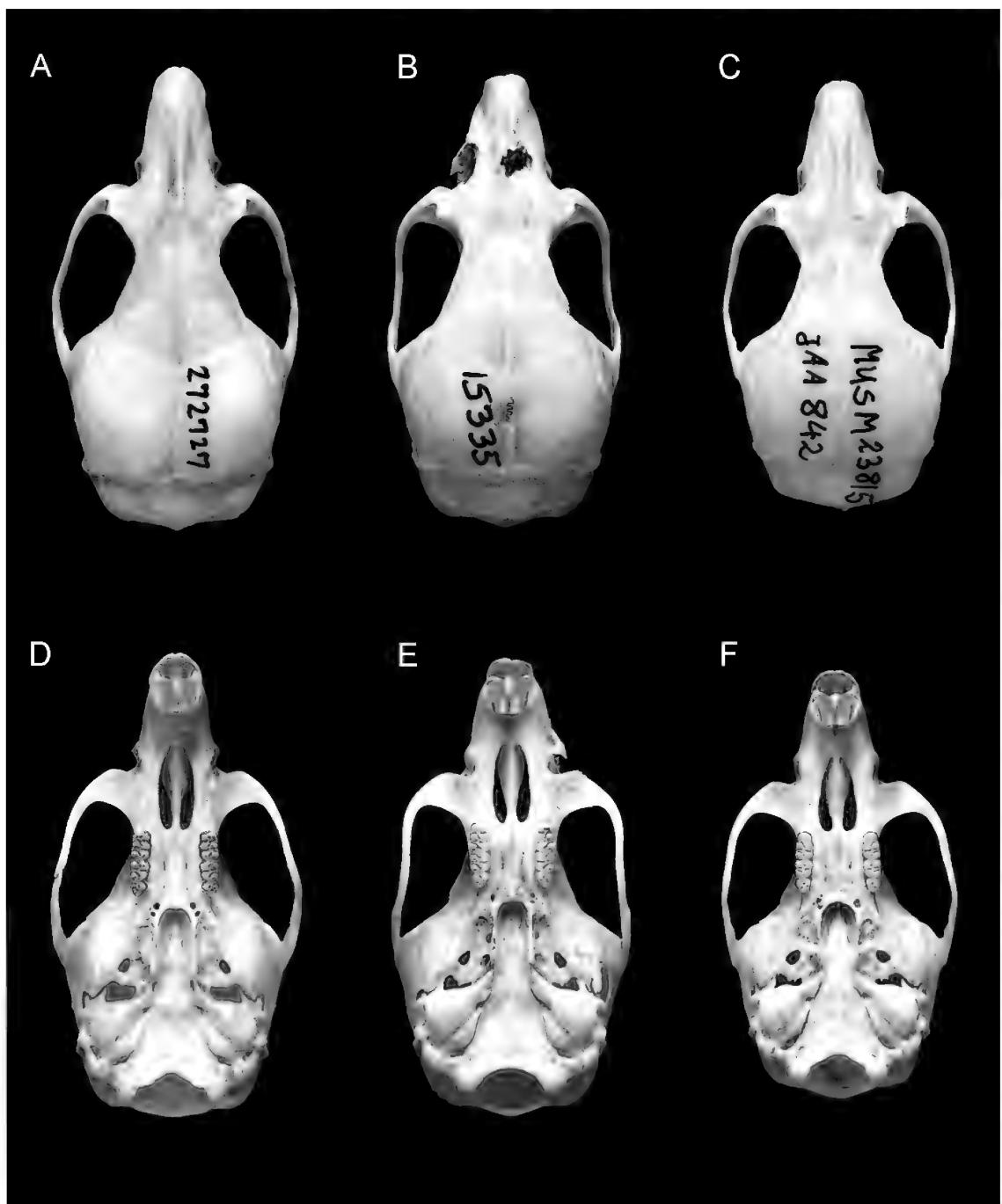
FIG. 26. Dorsal and ventral cranial views of *Oecomys bicolor* (**A**, **D**; AMNH 272727), *O. makampi* (**B**, **E**; MUSM 15335), and *O. nanus* (**C**, **F**; MUSM 23815). All views about ×2.5.

developed supraorbital branch of the stapedial artery (pattern 1 of Voss, 1988).

Our analyses of cytochrome *b* sequences from western Amazonian specimens with the phenotypic attributes of *Oecomys bicolor* recovered two haplogroups (figs. 25, 27): a strongly supported northern clade that includes specimens from eastern Ecuador (the type locality), northern Peru, and western Brazil; and a less strongly supported southern clade that includes specimens from southern Peru and western Brazil.[19] Widely separated geographic samples of the northern clade (including our series from the Yavarí-Ucayali interfluve) are remarkably similar morphometrically, especially in molar toothrow length (table 19), and we did not observe any noteworthy qualitative character variation among them. Uncorrected pairwise sequence differences at the cytochrome *b* locus within this clade are just 1.4%, on average, and we conclude that it represents a single taxon.

Specimens of the southern clade differ from specimens of the northern clade by an average value of about 5.7% in uncorrected pairwise sequence comparisons at the cytochrome *b* locus, but both clades have the same karyotype ($2n = 80$, $FN = 140$; Patton et al., 2000), and voucher specimens of the southern clade are not morphometrically distinguishable from northern-clade specimens. However, these clades appear to differ in occurrence of preputial glands. As noted earlier, macroscopic preputial glands are absent in dissected northern-clade specimens, but large preputial glands are present in several dissected southern-clade specimens, including MVZ 200963 (from western Brazil) and three specimens from Madre de Dios examined by Pacheco (2003).[20]

For the purposes of this report, we recognize the northern clade as *Oecomys bicolor* sensu stricto, but we have not undertaken a sufficiently detailed study of the nominal taxa currently synonymized with *O. bicolor* to formally restrict the application of this name. It is possible that the name *benevolens* Thomas, 1901 (with type locality in La Paz department, Bolivia) applies to the southern clade, but we have not examined the type, nor are any sequence data currently available from Bolivian material. The name *O. bicolor* is currently also applied to populations of small, white-bellied congeners from northeastern Amazonia and Central America, but, although other names are available for them, we are not prepared to recommend alternative binomial usage at this time.[21] In effect, a critical revision of the *O. bicolor* complex—ideally supported by broad geographic sampling of molecular sequences and morphology—is needed before relevant name changes can be recommended.

Diagnostic comparisons between *Oecomys bicolor* and other small sympatric congeners with self-white ventral fur are summarized in table 20 and discussed in the following accounts.

Ethnobiology: The usual Matses name for *Oecomys bicolor* is s̲h̲ubu pekid ("one that eats the house"). A regional variant term for this species is s̲h̲ubu kasëskid ("one that noisily chews on the thatch of the house"). A more succinct English rendering faithful to the meaning of both terms is "thatch-eater."

These semicommensal mice are much-despised pests. In addition to eating any vegetables or fruit left overnight in Matses homes (maize, ripe plantains, papayas, manioc, etc.), they chew noisily on the thatch at night, disturbing the residents' sleep. The Matses kill them by flushing them out of the thatch with a stick and then shooting them with makeshift arrows made of slivers of palm-frond petioles. They are sometimes killed in deadfall traps.

[19] Patton et al.'s (2000) specimens of *Oecomys bicolor* from the Rio Juruá include members of both clades.

[20] Weksler's (2006: table 5) scoring of accessory glands as present in *Oecomys bicolor* was based on Pacheco's (2003) dissections (M. Weksler, personal commun., 2021).

[21] We cannot, however, forbear from mentioning that Panamanian specimens (including the type series of *trabeatus* Allen and Barbour, 1923) have longer (8–10 mm) dorsal fur and relatively longer tails (LT/HBL = 1.20–1.31) than typical (western Amazonian) specimens of *Oecomys bicolor*, from which they also differ in several aspects of cranial morphology.
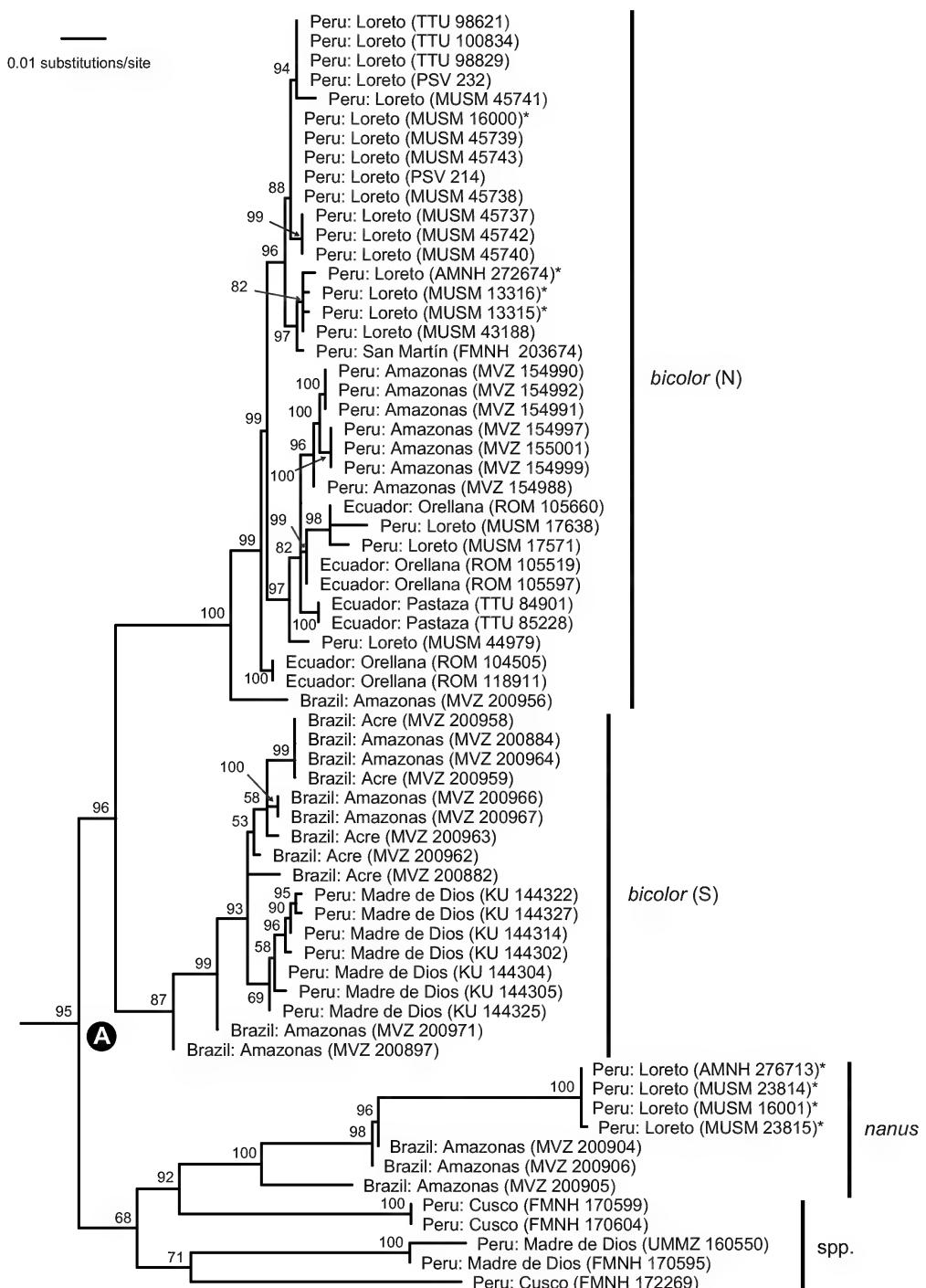
FIG. 27. Relationships among 66 cytochrome *b* sequences comprising node A (fig. 25), including *Oecomys bicolor*, *O. nanus*, and several unidentified sequences (see text). Asterisks (*) identify sequences obtained from specimens collected in the Yavarí-Ucayali interfluve. Terminals are labelled with country, next-largest administrative unit (state/department/province), and museum catalog number of specimens listed in appendix 3.

TABLE 19

External and Craniodental Measurements (mm) and Weights (g) of Specimens from Three Populations of the Northern Clade of *Oecomys bicolor*

	Yavarí-Ucayali interfluve[a]	Northern Loreto[b]	Eastern Ecuador[c]
HBL	102 ± 5 (95–110) 11	105 ± 6 (96–115) 11	99 ± 12 (82–117) 9
LT	111 ± 9 (90–122) 11	107 ± 6 (97–115) 11	110 ± 9 (97–121) 9
HF	23 ± 1 (19–24) 12	22 ± 1 (19–23) 14	22 ± 1 (21–23) 10
Ear	14 ± 1 (12–15) 10	13 ± 1 (11–14) 13	14 ± 1 (12–15) 7
CIL	24.4 ± 1.0 (23.0–25.8) 11	24.5 ± 0.6 (23.6–25.6) 13	24.2 ± 1.2 (22.1–25.6) 10
LD	7.0 ± 0.3 (6.4–7.6) 12	7.1 ± 0.3 (6.6–7.6) 14	6.9 ± 0.5 (5.9–7.3) 10
LM	3.8 ± 0.1 (3.7–4.0) 14	3.9 ± 0.1 (3.8–4.0) 14	3.8 ± 0.1 (3.7–3.9) 13
BM1	1.1 ± 0.0 (1.1–1.2) 14	1.1 ± 0.0 (1.1–1.1) 14	1.1 ± 0.0 (1.1–1.2) 13
LIF	4.7 ± 0.3 (4.1–5.0) 12	4.6 ± 0.2 (4.4–4.9) 14	4.4 ± 0.2 (4.1–4.7) 10
BIF	2.1 ± 0.1 (1.9–2.3) 12	2.1 ± 0.1 (1.9–2.3) 14	2.1 ± 0.1 (1.8–2.3) 11
BPB	2.7 ± 0.2 (2.5–3.0) 12	2.8 ± 0.2 (2.5–3.1) 14	2.6 ± 0.2 (2.4–2.9) 10
BZP	2.2 ± 0.1 (2.0–2.5) 12	2.2 ± 0.1 (1.9–2.4) 14	2.2 ± 0.1 (2.0–2.4) 11
LIB	4.8 ± 0.2 (4.5–5.1) 12	4.8 ± 0.2 (4.5–5.2) 14	4.7 ± 0.2 (4.5–4.9) 11
ZB	14.3 ± 0.5 (13.5–15.4) 12	14.2 ± 0.5 (13.2–15.1) 13	14.0 ± 0.6 (13.1–15.0) 11
LR	7.7 ± 0.3 (7.3–8.4) 12	7.9 ± 0.3 (7.3–8.3) 13	7.7 ± 0.3 (7.0–8.1) 9
Weight	32 ± 5 (25–39) 12	33 ± 5 (26–42) 13	27 ± 7 (19–39) 7

[a] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 268257, 268258, 272674, 272710, 272724, 272727, 273064, 273096; MUSM 13315, 13316, 13318, 13319, 15333, 15334.

[b] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: TTU 98621, 98766, 98829, 100834, 124942, 124943, 124945, 124947, 124949–124952, 124954, 124960.

[c] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 67404, 67504; BMNH 7.1.1.96 (holotype); ROM 104505, 105519, 105597, 105560, 106153, 118873, 118884, 118911; TTU 84901, 85228.

Matses natural history: Şhubu pekid is small and reddish with a white belly. It is found in the forest and in Matses homes, where it can become very numerous. It makes its nest where it cannot be seen in the thatch, often right at the ridgepole of the house. It also makes nests in containers where clothes that are not frequently used are stored. It chews up the clothes when it makes its nest there. It is nocturnal. It gives birth in the roof thatch and may persist for several generations in the house. It chews thatch noisily. It eats plantains and any food, including meat, that the Matses bring into the house, whether it be food for later consumption or leftovers from the evening meal, including the mesocarp of the isan palm (*Oenocarpus bataua*). In the forest they eat dicot tree fruits.

Remarks: Fifteen specimens of *Oecomys bicolor* from Nuevo San Juan are accompanied by habitat data; of these, 11 (73%) were taken in Matses houses (either caught by hand or trapped). Of the four remaining specimens, one was shaken from a liana where it was perched about 3 m above the ground at night in primary floodplain forest, another was trapped at an unrecorded height above the ground in primary liana forest, a third was shot high in a tree at night in primary hillside forest, and the last was shot at night at an unrecorded height in hilltop secondary vegetation.

TABLE 20

Morphological and Chromosomal Comparisons among Three Small Species of *Oecomys*
with Self-white Ventral Fur from the Yavarí-Ucayali Interfluve

	O. bicolor	*O. makampi*	*O. nanus*
Dorsal fur (length)	4–6 mm	7–9 mm	6–7 mm
Terminal tail hairs	2–5 mm	—	6–9 mm
Tail ratio (LT/HBL)	1.07 ± 0.09	—	1.15 ± 0.08
Caudal scale-rows/cm	19–24	15–17	17–19
Preputial glands	absent	small	large
Alisphenoid strut	usually absent	present	present or absent
Subsquamosal fenestra	large & patent	small, not patent	small & patent
Upper molars (crown length, LM)	3.7–4.0 mm	3.8 mm	3.3–3.7 mm
Least interorbital breadth (LIB)	4.5–5.1 mm	5.2–5.3 mm	4.5–4.9 mm
Breadth of rostrum (BR)	4.6–5.5 mm	5.9 mm	4.6 –5.1 mm
Karyotype	2n = 80	unknown	2n = 86–90?

Oecomys nanus, new species

Figures 26C, 26F

Oecomys species: Patton et al., 2000: 126 (an
unnamed form distinguished from other
congeners by size and cytochrome *b*
sequence comparisons).

Type material and type locality: The
holotype, MUSM 23815, consists of the skull,
fluid-preserved body, and frozen tissues of an
adult male collected by Jessica Amanzo (original
number JAA 842) at Jenaro Herrera on 21 June
2003. The frozen tissues of the holotype are pre-
served in the Ambrose Monell Cryo Collection
at the American Museum of Natural History
with catalog number M-280569.

Other voucher material (*N* = 11): Jenaro
Herrera (AMNH 276699, 276713, 276722;
MUSM 5452, 5462, 16001, 16003, 23814, 23816–
23818). Two additional specimens from Jenaro
Herrera (ZMMU S-151007, -151012) examined
by the late G.G. Musser probably correspond to
this species (see below).

Other specimens examined (*N* = 3): **Bra-
zil**—*Amazonas*, Colocação Vira-Volta on left
bank of Rio Juruá (MVZ 200906), Lago Vai-

Quem-Quer on right bank of Rio Juruá (MVZ
200905), Seringal Condor on left bank of Rio
Juruá (MVZ 200904).

Description: *Oecomys nanus* is one of the
smallest species in the genus, with recorded non-
pregnant adult weights consistently less than or
equal to 30 g. The adult dorsal pelage is grizzled
reddish-brown and 6–7 mm long at midback. The
ventral pelage is self-white (the hairs white to the
roots) from chin to anus, but two specimens
(MUSM 23816, MVZ 200905) have narrow (ca. 3
mm wide) lateral zones of gray-based hairs
between the fore- and hind legs. The hind feet are
covered dorsally with short, pale hairs, but most
specimens have indistinctly darker metatarsal
markings; the ungual tufts are neither dense
enough nor long enough to conceal the claws in
our Peruvian material, but one Brazilian specimen
(MVZ 200905) has long and dense ungual tufts on
digits II–V. The tail is unicolored (dark above and
below), about 115% of head-and-body length (on
average) and bears a pencil of apical hairs that are
6–9 mm long. We counted 17–19 scale-rows/cm
on four fluid-preserved specimens. In four dis-
sected adult male specimens (AMNH 276699,
276722; MUSM 23814, 23815) the preputial
glands are very large, extending beyond the ven-

tral flexure of the penis to lie between the skin and the abdominal musculature; measured from the free margin of the prepuce to their distal margin, these glands are 9–12 mm long, and they are visible externally as paired subcutaneous swellings just anterior to the penis.

The skull is diagnostically small in most measured dimensions (table 21). In dorsal cranial view the base of the rostrum is flanked by very shallow zygomatic notches and, as in other congeneric species, the interorbital region is beaded and strongly convergent anteriorly. Postorbital processes are absent, and the temporal crests (marking the dorsalmost origin of the temporalis muscle) are only weakly developed. In ventral view the incisive foramina are moderately long relative to diastemal length (LIF/LD = 0.63 ± 0.02), and sphenopalatine vacuities are absent (except in MVZ 200905). The alisphenoid strut (separating the buccinator-masticatory and accessory oval foramina) is bilaterally absent in seven adult skulls and bilaterally present in four others. The carotid circulation is complete, with a well-developed supraorbital ramus of the stapedial artery (pattern 1 of Voss, 1988). The tegmen tympani usually does not contact the squamosal, subsquamosal fenestrae are consistently present and patent (opening into the endocranial space without bony obstruction), and the mastoid capsules are usually fenestrated. The molar dentition qualitatively resembles those of other congeneric species and seems to lack any diagnostically useful traits.

Three Brazilian specimens karyotyped by Patton et al. (2000: 127) had $2n = 86$ chromosomes, but an even higher diploid number ($2n = 90$) was reported by Sokolov and Malygin (1994) from a taxon they identified as "*Oecomys bicolor*?" collected at Jenaro Herrera. The late G.G. Musser (personal commun.) measured two ZMMU specimens from Jenaro Herrera that might have been the ones karyotyped by Sokolov and Malygin; both had short (3.4–3.6 mm) molar toothrows—within the range of dental variation we attribute to *O. nanus*. However, we have not personally examined this material, so the attribu-

tion of Sokolov and Malygin's $2n = 90$ karyotype to the present species is uncertain.

VARIATION: We refer the three Brazilian specimens that Patton et al. (2000) called "*Oecomys* species" to *O. nanus* despite modest-to-substantial mtDNA sequence divergence (ca. 2.9%–7.1%, uncorrected, at the cytochrome *b* locus) because those specimens form a strongly supported clade with our material (fig. 27), and because the associated voucher material is morphometrically and qualitatively similar (with the apparently minor exceptions noted above). Although we acknowledge the possibility that the Brazilian and Peruvian specimens differ karyotypically (see above), it seems useful to have a name for the clade to which they both belong.

COMPARISONS: *Oecomys nanus* is smaller than sympatric *O. bicolor* (although there is some overlap in all measured dimensions; table 21), and it has longer fur (6–7 mm versus 4–6 mm) and a longer pencil of apical caudal hairs (6–9 mm versus 2–5 mm). Additionally, these species differ conspicuously in preputial gland morphology (very large in *O. nanus*, but macroscopically absent in *O. bicolor* sensu stricto), karyotypes ($2n = 86$–90? versus $2n = 80$), and in mtDNA sequence comparisons (ca. 7.8%, uncorrected, at the cytochrome *b* locus; table 18).

The only currently recognized congener that resembles *Oecomys nanus* in size is the Guianan species *O. rutilus* Anthony, 1921. In fact, despite their wide geographic separation, *O. nanus* and *O. rutilus* are morphometrically indistinguishable, with homologous measurement means that differ by only a few tenths of a millimeter (table 22). *Oecomys rutilus* also resembles *O. nanus* in external appearance, with long (6–8 mm) reddish-brown dorsal fur, self-white ventral fur, and a long-penciled tail (Voss et al., 2001: 109–116). The only craniodental difference we observed in side by side comparisons is that the zygomatic notches are so shallow in *O. nanus* as to be almost inapparent in dorsal view, whereas the zygomatic notches are visibly deeper and wider in *O. rutilus* (although not sufficiently so for the difference to be measurable). Like the specimens
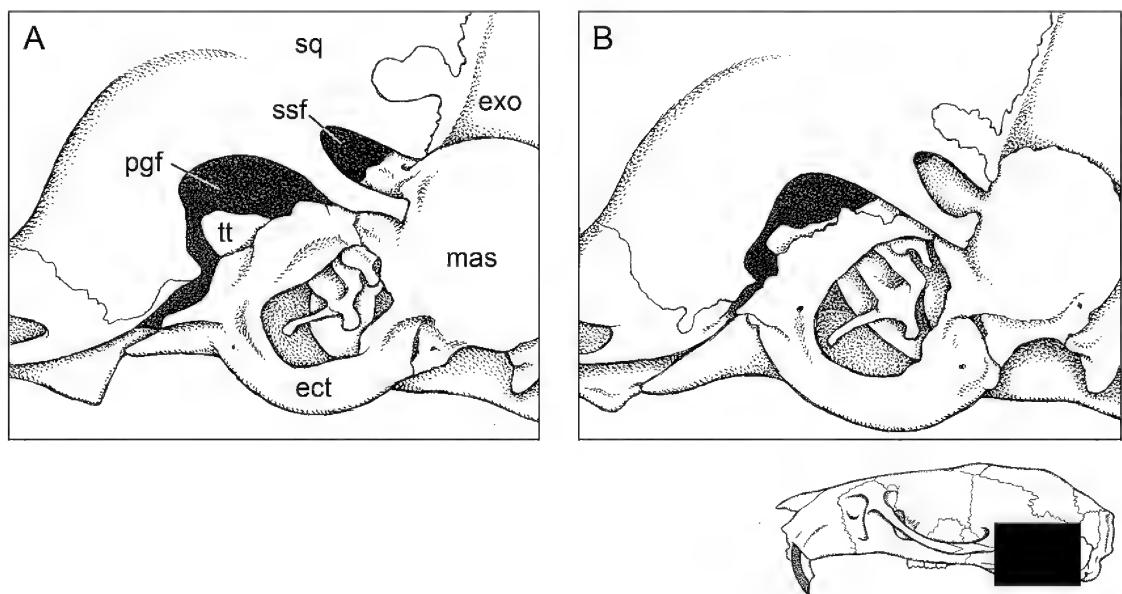
FIG. 28. Lateral view of left auditory region of *Oecomys bicolor* (**A**, AMNH 272727) and *O. makampi* (**B**, MUSM 11210), illustrating species difference in morphology of the subsquamosal fenestra (**ssf**), which is large and always patent in *O. bicolor*, but which is smaller and mostly occluded with bone in *O. makampi*. Other abbreviations: **ect**, ectotympanic; **exo**, exoccipital; **mas**, mastoid exposure of petrosal (coossified with ecto-tympanic); **pgf**, postglenoid foramen; **sq**, squamosal; **tt**, tegmen tympani (of petrosal).

we dissected of *O. nanus*, dissected male specimens of *O. rutilus* (AMNH 266561, 267584, 267586, 267588–267590) have large preputial glands. Despite such morphological similarities, karyotyped specimens of *O. rutilus* have $2n = 54$ chromosomes (Gomes et al., 2016)—16 fewer diploid pairs than the Brazilian specimens of *O. nanus* karyotyped by Patton et al. (2000) and 19 pairs fewer than the karyotype reported from Jenaro Herrera by Sokolov and Malygin (1994)—and phylogenetic analyses of mtDNA sequence data suggest that these species are not closely related (Suárez-Villota et al., 2018).[22]

Curiously, our phylogenetic analysis (fig. 27) recovered *Oecomys nanus* as the robustly supported sister taxon of an unnamed species repre-

sented by two specimens from southeastern Peru (FMNH 170599, 170604). The latter are much larger than *O. nanus* in all external and craniodental dimensions (e.g., LM = 4.6–4.7 mm), and they have partially gray-based ventral fur, very long (9–11 mm) dorsal fur, long ungual tufts, and narrow interorbital regions. The average pairwise uncorrected sequence difference at the cytochrome *b* locus between *O. nanus* and this unnamed taxon is 6.9%. No other taxon appears to be closely related to *O. nanus* based on our mtDNA sequence analyses.

ETYMOLOGY: The species name is Latin for "dwarf," a noun standing in apposition to the generic name.

ETHNOBIOLOGY: This species is not known to occur in Matses territory.

MATSES NATURAL HISTORY: The Matses have no knowledge of this species.

REMARKS: Of the eight specimens of *Oecomys nanus* collected in 2003 at Jenaro Herrera, seven were taken in pitfalls in swampy primary

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[22] *Oecomys nanus* is represented in Suárez-Villota et al.'s (2018: fig. 1) phylogenetic results by the cytochrome *b* sequence labelled "*Oecomys* sp. JUR 354," which was obtained by Patton et al. (2000) from the specimen now cataloged as MVZ 200905. Note, however, that none of the internal nodes separating *O. nanus* and *O. rutilus* in Suárez-Villota et al.'s phylogeny is strongly supported.

TABLE 21

**External and Craniodental Measurements (mm) and Weights (g) of Three Species of
Small *Oecomys* with Self-white Ventral Fur from the Yavarí-Ucayali Interfluve**

	O. bicolor[a]	*O. makampi*[b]	*O. nanus*[c]
HBL	102 ± 5 (95–110) 11	111, 99	92 ± 8 (75–100) 8
LT	111 ± 9 (90–122) 11	—, —	100 ± 8 (92–114) 8
HF	23 ± 1 (19–24) 12	22, 22	21 ± 1 (18–22) 8
Ear	14 ± 1 (12–15) 10	—, 14	14 ± 1 (12–15) 7
CIL	24.4 ± 1.0 (23.0–25.8) 11	25.2, 24.4	22.4 ± 0.8 (21.0–24.0) 10
LD	7.0 ± 0.3 (6.4–7.6) 12	7.1, 6.6	6.3 ± 0.3 (5.9–7.0) 10
LM	3.8 ± 0.1 (3.7–4.0) 14	3.8, 3.8	3.5 ± 0.1 (3.3–3.7) 12
BM1	1.1 ± 0.0 (1.1–1.2) 14	1.1, 1.1	1.0 ± 0.0 (0.9–1.1) 12
LIF	4.7 ± 0.3 (4.1–5.0) 12	4.3, 4.5	4.0 ± 0.3 (3.5–4.4) 10
BIF	2.1 ± 0.1 (1.9–2.3) 12	2.1, 2.2	2.0 ± 0.1 (1.7–2.2) 10
BPB	2.7 ± 0.2 (2.5–3.0) 12	2.9, 2.7	2.5 ± 0.2 (2.4–2.8) 10
BZP	2.2 ± 0.1 (2.0–2.5) 12	2.2, 2.3	1.8 ± 0.2 (1.6–2.2) 10
LIB	4.8 ± 0.2 (4.5–5.1) 12	5.3, 5.2	4.7 ± 0.2 (4.5–5.1) 10
ZB	14.3 ± 0.5 (13.5–15.4) 12	15.0, 14.0	13.1 ± 0.7 (12.4–14.1) 10
LR	7.7 ± 0.3 (7.3–8.4) 12	7.7, 7.9	7.0 ± 0.4 (6.4–7.6) 10
BR	5.1 ± 0.3 (4.6–5.5) 11	5.9, —	4.9 ± 0.2 (4.6–5.1) 5
Weight	32 ± 5 (25–39) 12	39, 45[d]	26 ± 4 (18–30) 8

[a] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 268257, 268258, 272674, 272710, 272724, 272727, 273064, 273096; MUSM 13315, 13316, 13318, 13319, 15333, 15334.

[b] Measurements and weights of MUSM 11210 and 15335 (the holotype).

[c] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 276699, 276713, 276722; MUSM 5452, 5456, 16001, 16003, 23814–23818.

[d] Pregnant.

forest and one was taken in a Victor snap trap set on the ground in primary white-sand forest. Neither of these habitat types is found near Nuevo San Juan, so it is possible that this species is a habitat specialist in our region. However, Patton et al.'s (2000) specimens were trapped in terra firme forest that was not growing on white sand, and unlike our exclusively terrestrial captures, two of their specimens were trapped high (9–13 m above the ground) in trees. In effect, nothing consistent is really known about either the habitat or the vertical distribution of this species, although its morphology (like that of other congeners) strongly suggests arboreal habits.

Oecomys makampi, new species

Figures 26B, 26E, 28B

TYPE MATERIAL AND TYPE LOCALITY: The holotype, MUSM 15335, consists of the fluid-preserved body, extracted skull, and frozen tissues of a pregnant adult female collected by David W. Fleck (original number DWF 730) at Nuevo San Juan on 31 August 1999. Because the specimen was collected with a shotgun, several morphological elements are damaged: on the skull, pellets damaged the rostrum, the left zygomatic plate, the right postorbital margin, and the left-lateral braincase; on the mandible, pellets smashed the left first molar and damaged the

TABLE 22

External and Craniodental Measurements (mm) and Weights (g) of *Oecomys nanus* and *O. rutilus*

	O. nanus[a]	*O. rutilus*[b]
HBL	92 ± 8 (75–100) 8	88 ± 9 (71–105) 31
LT	100 ± 8 (92–114) 8	100 ± 9 (80–113) 30
HF	21 ± 1 (18–22) 8	21 ± 1 (19–22) 40
Ear	14 ± 1 (12–15) 7	15 ± 1 (13–17) 36
CIL	22.4 ± 0.8 (21.0–24.0) 10	21.7 ± 1.0 (18.9–24.2) 39
LD	6.3 ± 0.3 (5.9–7.0) 10	6.2 ± 0.4 (5.2–7.0) 39
LM	3.5 ± 0.1 (3.3–3.7) 12	3.3 ± 0.1 (3.0–3.5) 38
BM1	1.0 ± 0.0 (0.9–1.1) 12	1.0 ± 0.0 (0.9–1.1) 40
LIF	4.0 ± 0.3 (3.5–4.4) 10	3.8 ± 0.2 (3.3–4.4) 41
BIF	2.0 ± 0.1 (1.7–2.2) 10	1.9 ± 0.1 (1.6–2.3) 40
BPB	2.5 ± 0.2 (2.4–2.8) 10	2.5 ± 0.2 (2.1–2.9) 38
BZP	1.8 ± 0.2 (1.6–2.2) 10	2.0 ± 0.2 (1.6–2.3) 40
LIB	4.7 ± 0.2 (4.5–5.1) 10	4.5 ± 0.2 (4.0–5.0) 40
ZB	13.1 ± 0.7 (12.4–14.1) 10	12.9 ± 0.8 (10.7–14.3) 40
LR	7.0 ± 0.4 (6.4–7.6) 10	6.9 ± 0.4 (6.4–7.8) 27
Weight	26 ± 4 (18–30) 8	22 ± 4 (12–32) 30

[a] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 276699, 276713, 276722; MUSM 5452, 5456, 16001, 16003, 23814–23818.

[b] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 42910 [holotype], 142820, 257268, 266561, 266563, 267584–267591, 267745, 269121, 269828; MHNG 1992.055; MNHN 1983-400, 1995-3236, 1995-3237, 1998-1845, 1998-1846, 2001-2217–2221; ROM 103482, 107083–107085, 111580, 115776, 115786, 115787, 115813, 120571; USNM 448576, 579992–579995.

right angular process. Although the fluid-preserved body was not damaged by shot, the distal portion of the tail is missing from an earlier (healed) injury. The frozen tissues of the holotype are preserved in the Ambrose Monell Cryo Collection at the American Museum of Natural History with catalog number M-279890).

OTHER VOUCHER MATERIAL (*N* = 1): Nuevo San Juan (MUSM 11210).

OTHER SPECIMENS EXAMINED: None.

DESCRIPTION: The two known specimens of *Oecomys makampi*, both adults, are small (39–45 g) mice with long (7–9 mm) dorsal fur and entirely self-white ventral fur. The dorsal fur of the paratype has faded in preservative, but the dorsal fur of the holotype is rich reddish brown, and a clear, bright orange lateral line marks the transition from dorsal to ventral color zones along the flanks. The hind feet are covered dorsally with pale hairs that were probably orangish in life, and the ungual tufts are short (the hairs not extending distally to the tips of the claws. The tail is unicolored (dark above and below) with 15–17 scale-rows/cm; both specimens lack the distal part of the tail, so it is not known whether a pencil of long apical hairs was present, nor can we compute the ratio of tail length to head-and-body length.

The skull is small in all dimensions (table 21). In dorsal cranial view the rostrum is broad, and it is flanked by very shallow zygomatic notches. The interorbital region is broad and strongly beaded. Postorbital processes are absent, and the temporal crests (marking the dorsalmost origin of the temporalis muscle on the lateral braincase) are only weakly devel-
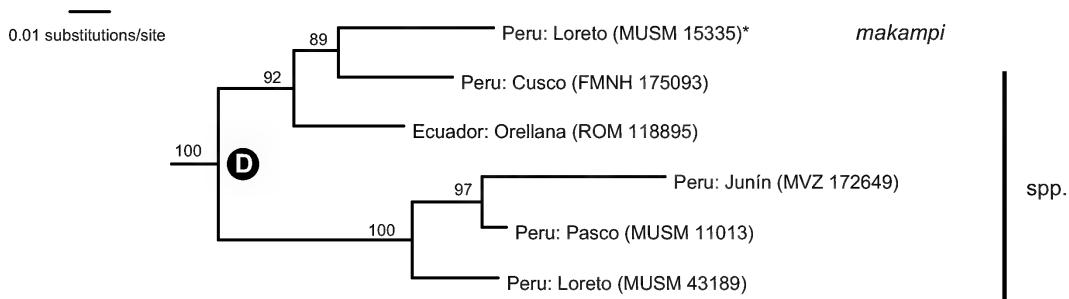
FIG. 29. Relationships among six cytochrome *b* sequences comprising node D (fig. 25), including *Oecomys makampi* and several unidentified sequences (see text). An asterisk (*) identifies the only sequence obtained from a specimen collected in the Yavarí-Ucayali interfluve. Terminals are labelled with country of origin, next-largest administrative unit (state/department/province), and museum catalog number of specimens listed in appendix 3.

oped. In ventral view, the incisive foramina are quite long relative to diastemal length (LIF/LD = 0.68) in the holotype but only moderately so (LIF/LD = 0.60) in the paratype; sphenopalatine vacuities are absent (the mesopterygoid roof is completely bony). Alisphenoid struts are bilaterally present in both specimens, and the stapedial arterial circulation is complete, with a well-developed supraorbital branch (pattern 1 of Voss, 1988). The subsquamosal fenestrae are small and almost completely occluded by bone in both specimens, which also lack contact between the tegmen tympani and the posterior edge of the squamosal (fig. 28B). The mastoid capsules are fenestrated.

The molar dentition appears to lack any taxonomically distinctive features.

COMPARISONS: *Oecomys makampi* differs externally from sympatric *O. bicolor* by its longer dorsal fur (7–9 mm versus 4–6 mm), presence of an orange lateral line separating the dorsal and ventral color zones (absent in *O. bicolor*), and larger caudal scales (as indexed by caudal scale rows/cm; table 20). Additionally, the male paratype has small preputial glands (one on either side, not extending beyond the ventral flexure of the penis), whereas preputial glands are macroscopically absent in *O. bicolor* (sensu stricto).

Oecomys makampi and *O. bicolor* overlap in most cranial measurements (table 21), but *O.*

makampi has a broader rostrum (BR = 5.9 mm versus 4.6–5.5 mm) and a wider interorbital region (LIB = 5.2–5.3 mm versus 4.5–5.1 mm) than *O. bicolor*, and both dimensions contribute to the distinctly different appearance of the anterior cranium in these species (fig. 26). Additionally, the subsquamosal fenestra (an open notch in the posterior margin of the squamosal) of *O. makampi* is small, and it is mostly occluded internally by a flange of the petrosal bone (fig. 28B), whereas the subsquamosal fenestra is substantially larger in *O. bicolor* and it is patent, opening onto the endocranial cavity (fig. 28A).

The average uncorrected pairwise sequence difference at the cytochrome *b* locus between *Oecomys makampi* and *O. bicolor* is 10.0% (table 18), and in our phylogenetic analysis these species are not sister taxa (fig. 25). Instead, *O. makampi* is strongly associated with sequences obtained from several specimens of small, white-bellied mice that it does not otherwise closely resemble (fig. 29). For example, FMNH 175093, a juvenile specimen from Cusco department in southeastern Peru, lacks an alisphenoid strut and has an upper molar toothrow that we estimate to be about 4.2 mm (about 10% larger than this dimension in *O. makampi*); the cytochrome *b* sequence that we obtained from this specimen differs from that of *O. makampi* by 5.0% (uncorrected). Although FMNH 175093 is possibly

referable to *O. phaeotis* (the holotype of which also lacks an alisphenoid strut and has similar molar dimensions), its immature morphology and the absence of sequence data from the type series of *O. phaeotis* preclude confident taxonomic inference.

The next-closest relative to *Oecomys makampi* in our molecular phylogeny is ROM 118895 an adult female from Orellana province, Ecuador. This specimen has an upper molar toothrow that is 3.4 mm (about 10% smaller than that of *O. makampi*), and it also differs from *O. makampi* by having large, patent subsquamosal fenestrae. The cytochrome *b* sequence we obtained from this specimen differs by 5.4% (uncorrected) from that of *O. makampi*. We are unable to associate ROM 118895 with any available name.

None of the other specimens that appear to be closely related to *Oecomys makampi* in our molecular phylogeny (MUSM 11013, MUSM 43189, MVZ 172649) closely resemble it morphologically, nor do they closely resemble one another, and their corresponding cytochrome *b* sequences suggest substantial genetic divergence: 8.1%–9.7% from *O. makampi* and 3.2%–5.8% from one another). None can be confidently associated with named taxa. The obvious implication of these observations is that there could be multiple undescribed species in this previously unsuspected clade.

ETYMOLOGY: The species name, a noun in apposition, is formed from the Matses word for rat (<u>maka</u>) combined with the suffix -<u>mpi</u>, meaning "small" (in effect, a mouse).

ETHNOBIOLOGY: The Matses do not recognize this species as distinct from *Oecomys bicolor* (which commonly infests their houses), and so have no particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

REMARKS: The holotype was shot at night in an abandoned swidden by a Matses hunter who provided no additional details. The paratype was trapped about 0.5 m above the ground on a fallen branch in primary upland forest.

Oecomys galvez, new species

Figures 30A, 30D, 31A, 32A

Oecomys trinitatis: Patton et al., 2000: 131 (a misidentification; not *Oryzomys trinitatis* Allen and Chapman, 1893).

HOLOTYPE: The holotype, MUSM 13320, consists of the skull, fluid-preserved body, and frozen tissues of an adult male collected by Robert S. Voss (original number RSV 2023) at Nuevo San Juan on 20 May 1998. The frozen tissues of the holotype are preserved in the Ambrose Monell Cryo Collection at the American Museum of Natural History with catalog number M-280496.

OTHER VOUCHER MATERIAL (*N* = 10): Jenaro Herrera (AMNH 276720; MUSM 16002, 23819), Nuevo San Juan (AMNH 273033, 273088, 273122; MUSM 15336–15339).

OTHER SPECIMENS EXAMINED (*N* = 15): **Brazil**—*Acre*, opposite Igarapé Porongaba on left bank of Rio Juruá (MVZ 200948); *Amazonas*, Barro Vermelho on left bank of Rio Juruá (MVZ 200949), Colocação Vira-Volta on left bank of Rio Juruá (MVZ 200953, 200954), Penedo on right bank of Rio Juruá (MVZ 200955). **Ecuador**—*Orellana*, 38 km S Pompeya Sur (ROM 105224, 118789, 118850), 42 km S Pompeya Sur (ROM 106145, 118868), 66 km S Pompeya Sur (ROM 105985, 105986), 76 km S Pompeya Sur (ROM 105321, 106068). **Peru**—*Loreto*, San Jacinto (KU 158192).

DESCRIPTION: *Oecomys galvez* is a large (41–75 g) species with 7–10 mm long, tawny-brownish dorsal fur and grayish-white ventral fur (the individual hairs have long gray bases and whitish tips). The transition from dorsal to ventral coloration is abrupt, without any intervening ochraceous line along the flanks. The medial metatarsus and the digits of the hind foot are covered dorsally with short, pale hairs, but the lateral metatarsus is usually covered with darker hairs. The ungual tufts are short and sparse, not concealing the claws on any of the pedal digits (fig. 31A). The tail is long
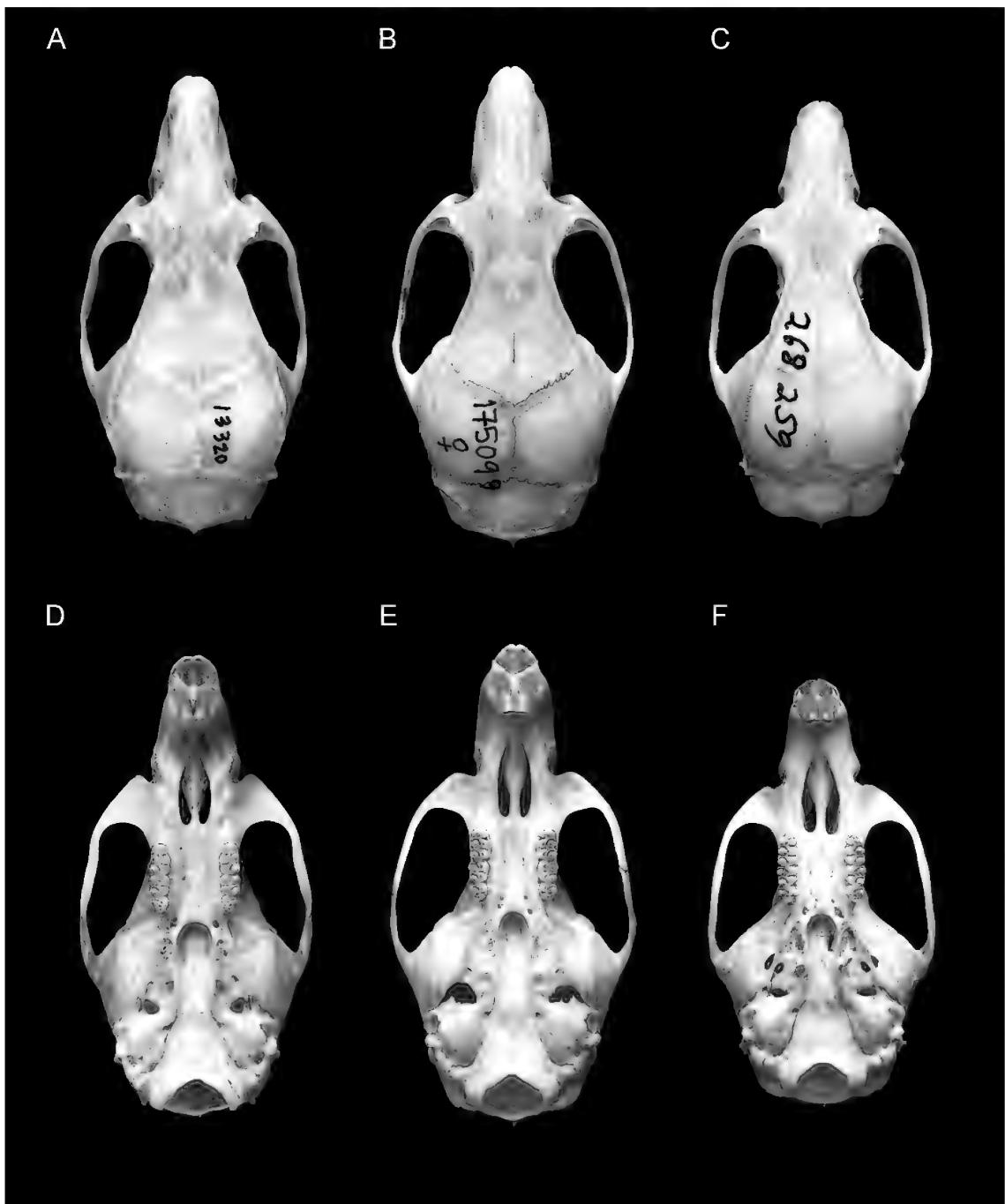
FIG. 30. Dorsal and ventral cranial views of *Oecomys galvez* (**A**, **D**; MUSM 13320), *O. superans* (**B**, **E**; FMNH 175099), and *O. roberti* (**C**, **F**; AMNH 265259). The specimen of *O. superans* is not from the Yavarí-Ucayali interfluve, although the species is expected to occur there.

(about 126% of head-and-body length, on average), unicolored (dark above and below), and lacks a terminal pencil (the apical hairs are ≤3 mm long); we counted 17–20 caudal scale rows/cm on several fluid-preserved specimens. The preputial glands are large, extending anteriorly beyond the ventral flexure of the penis.

In dorsal cranial view (fig. 30A) the rostrum is flanked by moderately deep zygomatic notches, and postorbital processes are absent; the temporal crests (marking the dorsal origin of the temporalis muscle) are only weakly developed on the parietal bones. In ventral cranial view (fig. 30B), the incisive foramina are diagnostically short (LIF/LD = 0.56 ± 0.04) and terminate well anterior to the alveoli of the first maxillary molars; in most specimens these foramina are widest posteriorly (behind the premaxillary-maxillary suture) and taper anteriorly. Sphenopalatine vacuities (paired openings in the bony roof of the mesopterygoid fossa) are consistently absent. Alisphenoid struts (separating the buccinator-masticatory and accessory oval foramina) are variable in this species: they are bilaterally present in eight specimens, bilaterally absent in another eight, and unilaterally present in two. The stapedial arterial circulation is complete, with a well-developed supraorbital branch (pattern 1 of Voss, 1988). The subsquamosal fenestrae are small but patent (exposing the interior braincase) in fewer than half the specimens we examined; in most specimens these fenestrae are either occluded internally by a bony flange of the petrosal, or they are absent altogether. The mastoid capsules are consistently unfenestrated.

The molar dentition seems to lack any distinctive features.

Karyotyped specimens of *Oecomys galvez* (originally identified as *O. trinitatis*; see below) include one from Jenaro Herrera reported by Sokolov and Malygin (1994) and four reported by Patton et al. (2000) from western Brazil; all had $2n = 58$ chromosomes. We have not seen the specimen from Jenaro Herrera (ZMMU
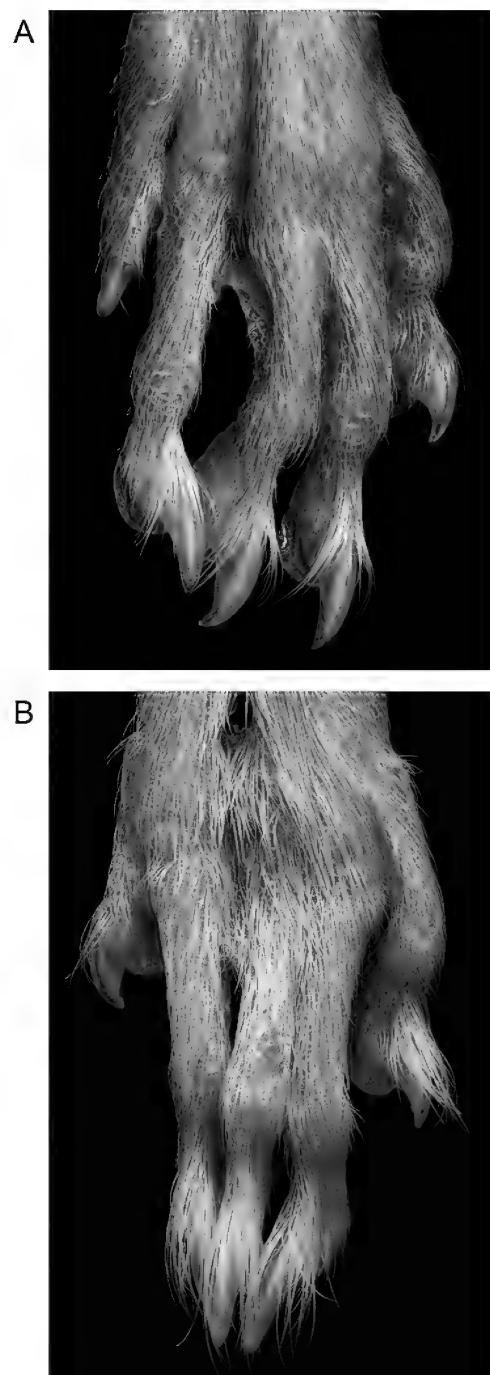

FIG. 31. Dorsal views of left hind feet of *Oecomys galvez* (**A**, MUSM 15338) and *O. trinitatis* (**B**, AMNH 188415) illustrating species difference in the development of ungual tufts (long hairs rooted at the bases of the claws).
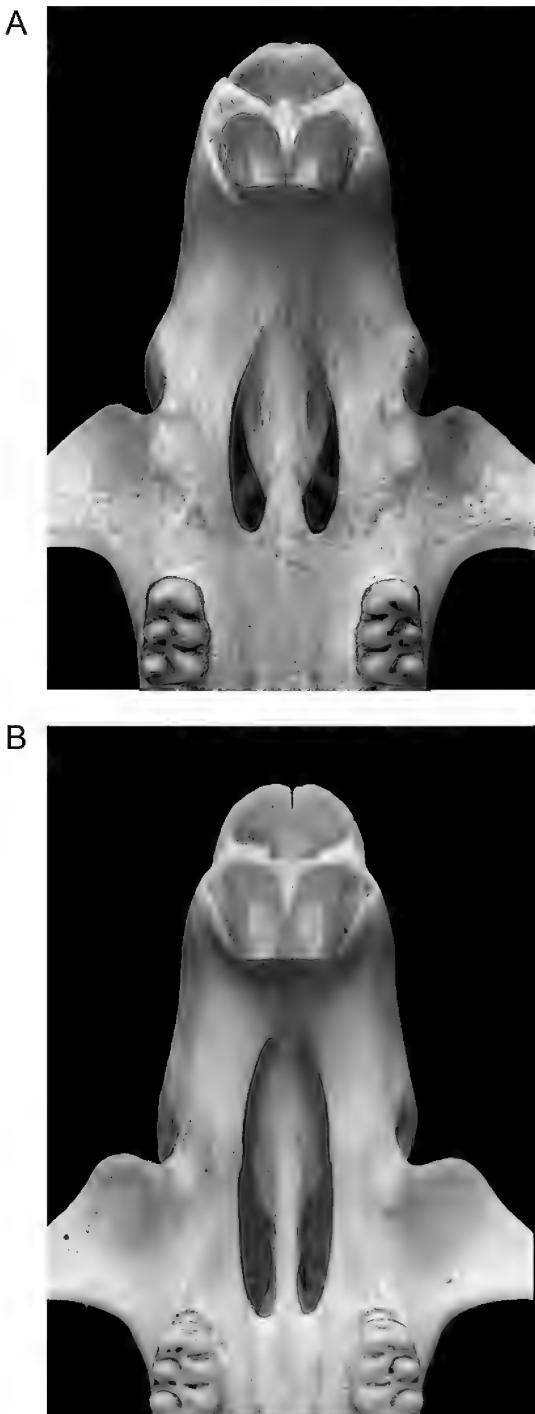
FIG. 32. Ventral views of diastemal palate of *Oecomys galvez* (**A**, MUSM 15337) and *O. trinitatis* (**B**, AMNH 186732) illustrating species differences in morphology of the incisive foramina.

S-151008), but it was examined by the late G.G. Musser, whose unpublished notes (in the AMNH Mammalogy archives) mentioned that it closely resembled Patton et al.'s Brazilian material.

VARIATION: Sequenced specimens that we refer to *Oecomys galvez* belong to two strongly supported mtDNA clades from opposite sides of the Amazon (fig. 33). However, representative specimens of these northern and southern haplogroups are morphometrically indistinguishable (table 23), and we were unable to find any consistent qualitative differences between these populations by visual comparisons of skins and skulls.

COMPARISONS: Specimens of *Oecomys galvez* from western Brazil were previously identified as *O. trinitatis* (Allen and Chapman, 1893) by the late G.G. Musser, whose recommended taxonomy of Brazilian *Oecomys* was adopted by Patton et al. (2000). Although no justification for this identification was provided, *O. galvez* and *O. trinitatis* both have gray-based ventral pelage, tails that lack a distinct pencil of long apical hairs, and deeper zygomatic notches than those of many other congeneric species. Additionally, *O. galvez* and *O. trinitatis* (sensu stricto)[23] are about the same size and overlap in all measured external and craniodental traits. Nevertheless, *O. trinitatis* differs from *O. galvez* in several morphological and chromosomal traits (table 24). Among other contrasts, *O. trinitatis* has longer dorsal fur, denser and longer ungual tufts on digits II–V of the hind foot (fig. 31B), and incisive

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[23] Carleton and Musser (2015: 417) acknowledged that their concept of *Oecomys trinitatis* was probably composite, and we agree. Therefore, we restricted our comparative sample to the following adult specimens from Trinidad (the type locality) and the adjacent continental mainland: **Trinidad and Tobago**—*Trinidad*, Bush Bush Forest (AMNH 185472, 186732, 186736, 188414), Caura (AMNH 7728/6113, BMNH 99.9.4.5), Maingot Estate (AMNH 174067), Princestown (AMNH 5943/4673 [holotype]). **Venezuela**—*Monagas*, 3–5 km NW Caripe (USNM 409875, 409876, 409878, 409879); *Sucre*, Campo Alegre (BMNH 0.5.1.11, 0.5.1.12, 0.5.1.18), La Hormiga (BMNH 0.5.1.13, 0.5.1.14), Latal (AMNH 69862, 69866–69868), Los Palmales (BMNH 2.3.6.52), Neverí (AMNH 69858, 69859), Quebrada Seca (BMNH 0.5.1.15; AMNH 14729, 14733, 14735), Spure (BMNH 0.5.1.16, 0.5.1.17).

TABLE 23

External and Craniodental Measurements (mm) and Weights (g) of *Oecomys galvez*

	Southern clade[a]	Northern clade[b]	Combined samples
HBL	129 ± 8 (116–140) 13	136 ± 11 (125–154) 5	131 ± 9
LT	162 ± 8 (146–174) 13	172 ± 8 (160–183) 5	165 ± 9
HF	28 ± 1 (27–29) 13	29 ± 0 (28–29) 6	28 ± 1
Ear	17 ± 1 (16–19) 12	17 ± 1 (16–20) 6	17 ± 1
CIL	30.3 ± 0.8 (28.5–31.3) 12	30.2 ± 1.0 (29.2–31.9) 6	30.2 ± 0.9
LD	9.0 ± 0.5 (8.0–9.6) 13	9.2 ± 0.3 (8.9–9.6) 6	9.1 ± 0.4
LM	5.2 ± 0.1 (5.0–5.5) 16	5.2 ± 0.1 (5.0–5.3) 10	5.2 ± 0.1
BM1	1.5 ± 0.0 (1.4–1.6) 16	1.5 ± 0.0 (1.4–1.6) 10	1.5 ± 0.0
LIF	5.1 ± 0.3 (4.6–5.5) 13	5.2 ± 0.3 (4.9–5.7) 6	5.1 ± 0.3
BIF	2.5 ± 0.2 (2.2–2.8) 13	2.6 ± 0.1 (2.5–2.7) 6	2.5 ± 0.2
BPB	3.4 ± 0.2 (3.0–3.7) 13	3.1 ± 0.1 (2.9–3.3) 6	3.3 ± 0.2
BZP	3.2 ± 0.2 (2.8–3.6) 13	3.1 ± 0.1 (3.0–3.2) 6	3.2 ± 0.2
LIB	5.8 ± 0.3 (5.4–6.2) 12	5.8 ± 0.3 (5.3–6.1) 6	5.8 ± 0.3
ZB	17.5 ± 0.5 (16.5–18.3) 12	17.3 ± 0.6 (16.8–18.3) 5	17.4 ± 0.5
LR	10.2 ± 0.4 (9.4–10.6) 13	10.7 ± 0.5 (10.0–11.5) 5	10.4 ± 0.5
Weight	62 ± 7 (51–75) 13	59 ± 11 (41–74) 6	61 ± 8

[a] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (from south of the Amazon in Peru and W Brazil): AMNH 273033, 273088, 273122, 276720; MUSM 13320, 15336–15339, 16002, 23819; MVZ 200948, 200949, 200953–200955.

[b] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series (from north of the Amazon in Peru and E Ecuador): KU 158192; ROM 105224, 105321, 105958, 105986, 106068, 106145, 118789, 118850, 118868.

foramina that are much longer in proportion to the diastema (fig. 32B). A single karyotyped individual of *O. trinitatis* from eastern Venezuela (USNM 448579) had 2n = 54 chromosomes, whereas *O. galvez* has 2n = 58 chromosomes based on our reidentification of Patton et al.'s (2000) material.

Peruvian specimens that closely resemble typical (Trinidadian/Venezuelan) *Oecomys trinitatis* include the holotype (BMNH 24.7.11.16) and a paratype (BMNH 24.7.11.17) of *O. osgoodi* Thomas, 1924, a nominal taxon that Carleton and Musser (2015: 414) treated as a junior synonym. The type series of *osgoodi* was collected at Moyobamba (in San Martín department), a locality in the Andean foothills almost 400 km west of our region, and we have examined additional specimens from foothill localities in Huá-

nuco (FMNH 24574, 24576) and Cusco (FMNH 175097). A cytochrome *b* sequence that we obtained from FMNH 175097 differs from sequences of *O. galvez* by 10.7% (table 18), and our phylogenetic analysis suggests that these taxa are not closely related (fig. 25).

Oecomys galvez also merits comparisons with *O. superans* Thomas, 1911, a morphologically similar western Amazonian species. *Oecomys galvez* and *O. superans* have broadly overlapping geographic ranges, and they have been collected sympatrically (although perhaps not syntopically) in eastern Ecuador (specimens at ROM), northern Peru (specimens at KU), and western Brazil (specimens at MVZ). Like *O. galvez*, *O. superans* has gray-based ventral pelage and a tail that lacks a distinct pencil of long apical hairs. Although *O. superans*, is larger (on average) than
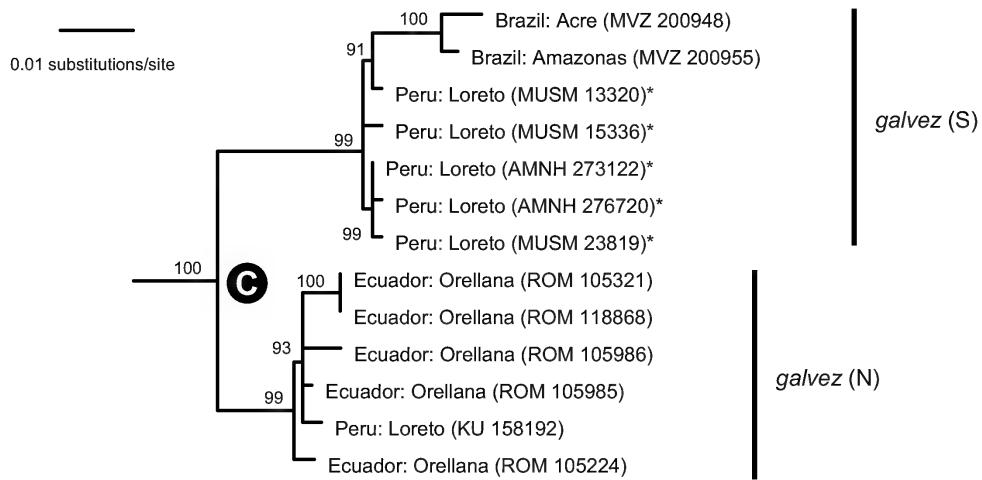
FIG. 33. Relationships among 13 cytochrome *b* sequences comprising node C (fig. 25), including both haplogroups of *Oecomys galvez* (see text). Asterisks (*) identify sequences obtained from specimens collected in the Yavarí-Ucayali interfluve. Terminals are labelled with country, next-largest administrative unit (state/department/province), and museum catalog number of specimens listed in appendix 3.

O. galvez in most external and craniodental dimensions (table 25), these species overlap in all external measurements, such that large specimens of *O. galvez* could be confused with small specimens of *O. superans*. However, side by side comparisons of museum skins suggest that *O. galvez* has finer, softer, and less coarsely grizzled dorsal fur than *O. superans*. Additionally, whereas the ventral pelage of *O. galvez* is always graybased whitish (the individual hairs with gray bases and white tips), more than half the specimens we examined of *O. superans* have graybased buffy ventral fur (the hair tips ranging from pale buff to almost orange). Lastly, the ungual tufts—clusters of hairs rooted at the bases of the claws on digits II–V of the hind foot—are always short and sparse in *O. galvez* (not reaching the ends of the claws and not dense enough to conceal them), whereas these tufts are usually longer and denser in *O. superans*. Despite such differences, we suspect that it might be impossible to distinguish these species in the field.

In dorsal cranial comparisons (fig. 30), *Oecomys galvez* has deeper zygomatic notches than *O. superans*, a more tapering rostrum, and a relatively broader interorbital region. In ventral cra-

nial view, *O. galvez* has distinctively shorter incisive foramina (5.1 ± 0.3 mm versus 6.2 ± 0.4 mm); the incisive foramina are also shorter in proportion to the diastema in *O. galvez* than they are in *O. superans* (LIF/LD = 0.56 ± 0.04 versus 0.66 ± 0.03). Lastly, the alisphenoid strut is bilaterally present in about half our examined specimens of *O. galvez*, but it is only rarely present unilaterally (never bilaterally) in *O. superans*. Other cranial differences are inapparent, despite the wide divergence of these species in mtDNA sequences (fig. 25, table 18) and karyotypes ($2n$ = 58 versus $2n$ = 80; Patton et al., 2000).[24]

[24] Specimens of *Oecomys superans* examined for these comparisons include the following specimens: **Brazil**—*Amazonas*, Altamira on right bank of Rio Juruá (MVZ 200945), Penedo on right bank of Rio Juruá (MVZ 200944). **Ecuador**—*Napo*, near the Río Napo (BMNH 34.9.10.116, 34.9.10.117, 34.9.10.208); *Orellana*, near the Río Suno (BMNH 34.9.10.114, 34.9.10.115), 18 km S Pompeya Sur (ROM 106144), 38 km S Pompeya Sur (ROM 118851); *Pastaza*, Canelos on Río Bobonaza (BMNH 11.7.19.12 [holotype], 11.7.19.13); *Zamora-Chinchipe*, Zamora (AMNH 36560). **Peru**—*Amazonas*, Huampami on Río Cenepa (MVZ 155004, 155006, 155008, 155012; *Cusco*, 15.9 km SW Pilcopata (FMNH 175099); *Loreto*, San Jerónimo (BMNH 28.5.2.187–28.5.2.190), Sarayacu on Río Ucayali (AMNH 76175, 76298); *Madre de Dios*, Hacienda Erica (MVZ 166698), Reserva Cusco Amazónico (KU 144332); *Pasco*, Bermudas Loma Linda (AMNH 213540, 213541, 232140), Nevatí Mission (AMNH 231127), San Pablo

TABLE 24

Morphological and Chromosomal Comparisons between *Oecomys galvez* and *O. trinitatis*

	O. galvez	*O. trinitatis*[a]
Dorsal fur (length)	usually 7–10 mm	usually 12–14 mm
Ventral fur (color)	gray-based white	usually gray-based buffy[b]
Ungual tufts	short & sparse	very long & dense
Alisphenoid strut	present or absent	always present
Incisive foramen ratio (LIF/LD)	0.56 ± 0.04	0.72 ± 0.02
Karyotype	$2n = 58$	$2n = 54$

[a] Sensu stricto (from Trinidad and eastern Venezuela; see text).
[b] Specimens from the Venezuelan mainland have gray-based buffy ventral fur, but Trinidadian specimens have gray-based whitish ventral fur.

Oecomys galvez also resembles a sympatric taxon that we provisionally recognize as a member of the *O. roberti* complex (see below). Unlike typical *O. roberti*, which has self-white ventral fur (the individual hairs pure white from root to tip), the local phenotype has gray-based whitish ventral fur like that of *O. galvez*. Additionally, this local form of *O. roberti* resembles *O. galvez* by its similarly grizzled tawny-brown pelage, unicolored tail lacking a pencil of long apical hairs, and similar external dimensions (table 25). In fact, we suspect that these taxa might be externally indistinguishable, such that field researchers in our region could be confounded by as many as three difficult-to-distinguish sympatric congeners (including *O. superans*, an expected species; see appendix 5).

Oecomys galvez and *O. roberti* are also similar craniodentally. In fact, we have not discovered any trait of the cranium or dentition by which they can be infallibly distinguished across the ranges of both species. In our region, however, *Oecomys galvez* usually has larger molars than *O. roberti* (LM = 5.0–5.5 mm versus 4.7–5.0 mm) and always has shorter incisive foramina in proportion to its diastema (LIF/LD = 0.54–0.58 versus 0.60–0.67). Skulls of *O. galvez* also tend to have deeper zygomatic notches than those of *O. roberti* (fig. 30), a contrast that is difficult to mea-

sure, although it is correlated with breadth of the zygomatic plate (BZP). In effect, skulls can be sorted by gestalt, but not without risk of error. These unsatisfactory morphological results might be considered grounds for questioning the distinctness of these taxa were it not for their substantial sequence divergence (fig. 25, table 18) and karyotypic differences ($2n = 56$ versus $2n = 80$; Patton et al., 2000).

ETYMOLOGY: For the Río Gálvez, near which the holotype was collected on the right (south) bank.

ETHNOBIOLOGY: The Matses do not recognize this species and so have no particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no knowledge of this species.

REMARKS: *Oecomys galvez* appears to be a semiarboreal primary forest species that favors well-drained sites in our region, but it is not a habitat specialist. Of the 10 specimens accompanied by ecological data from Nuevo San Juan and Jenaro Herrera, four were shot at night in trees or on lianas, three were caught by hand at night on trees and on a liana, one was taken by hand in the daytime from its nest among the branches of a fallen tree; one was taken in a pitfall trap, and one was trapped on the ground. Six captures were recorded from primary upland forest, one in primary floodplain forest, one in primary swamp forest, and one in primary white sand

(AMNH 231131, 231132); *San Martín*, Pachiza on upper Río Huallaga (AMNH 98256).

TABLE 25

External and Craniodental Measurements (mm) and Weights (g) of
Oecomys galvez, O. superans, and *O. roberti*

	O. galvez[a]	*O. superans*[b]	*O. roberti*[c]
HBL	131 ± 9 (116–154) 17	145 ± 11 (122–160) 17	128 ± 9 (109–147) 24
LT	165 ± 9 (146–183) 17	171 ± 12 (142–199) 17	156 ± 12 (135–176) 24
HF	28 ± 1 (27–29) 18	30 ± 1 (28–33) 21	27 ± 1 (25–29) 26
Ear	17 ± 1 (16–20) 17	17 ± 1 (15–20) 17	17 ± 1 (15–20) 24
CIL	30.2 ± 0.9 (28.5–31.9) 18	32.3 ± 1.3 (30.1–34.4) 25	29.3 ± 1.3 (26.4–31.8) 25
LD	9.1 ± 0.4 (8.0–9.6) 19	9.4 ± 0.4 (8.6–10.4) 29	8.6 ± 0.4 (7.9–9.6) 26
LM	5.2 ± 0.1 (5.0–5.5) 25	5.4 ± 0.2 (5.1–6.1) 29	5.0 ± 0.1 (4.7–5.3) 27
BM1	1.5 ± 0.0 (1.4–1.6) 25	1.5 ± 0.1 (1.4–1.7) 29	1.4 ± 0.0 (1.3–1.5) 27
LIF	5.1 ± 0.3 (4.6–5.7) 19	6.2 ± 0.4 (5.4–6.7) 29	5.2 ± 0.3 (4.7–5.8) 26
BIF	2.5 ± 0.2 (2.2–2.8) 19	2.8 ± 0.2 (2.3–3.3) 29	2.6 ± 0.2 (2.0–3.0) 26
BPB	3.3 ± 0.2 (2.9–3.7) 19	3.4 ± 0.2 (3.0–3.9) 28	3.3 ± 0.2 (2.9–3.8) 25
BZP	3.2 ± 0.2 (2.8–3.6) 19	3.3 ± 0.3 (2.9–3.9) 29	3.0 ± 0.2 (2.5–3.4) 27
LIB	5.8 ± 0.3 (5.3–6.2) 18	5.9 ± 0.4 (5.0–7.1) 29	5.5 ± 0.3 (5.0–6.2) 24
ZB	17.4 ± 0.5 (16.5–18.3) 17	18.1 ± 0.9 (16.7–19.9) 25	17.2 ± 0.8 (15.8–18.7) 24
LR	10.4 ± 0.5 (9.4–11.5) 18	11.2 ± 0.6 (10.3–12.3) 26	10.0 ± 0.5 (9.1–10.9) 24
Weight	61 ± 8 (41–75) 19	87 ± 13 (72–115) 11	57 ± 9 (42–79) 26

[a] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the combined samples from table 23.

[b] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 36560, 76175, 76298, 98256, 213540, 213541, 231127, 231131, 231132, 232140; BMNH 11.7.19.12, 11.7.19.13, 28.5.2.187, 28.5.2.189, 28.5.2.190, 34.9.10.114–34.9.10.117, 34.9.10.208, 1954.475; FMNH 175099; KU 144332; MVZ 155004, 155008, 166698, 200944, 200945; ROM 106144.

[c] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the combined samples from table 27.

forest. Patton et al.'s (2000: 132) capture data for this species (which they identified as *O. trinitatis*; see above) similarly suggest semiarboreal habits in diverse primary-forest situations.

Oecomys roberti (Thomas, 1903)

Figures 30C, 30F

VOUCHER MATERIAL (*N* = 7): Jenaro Herrera (AMNH 276701), Nuevo San Juan (AMNH 268259, 268262, 273112, 273119; MUSM 11215, 15340).

UNVOUCHERED RECORDS: None.

OTHER SPECIMENS EXAMINED (*N* = 46): **Brazil**—*Amazonas*, Altamira on right bank of Rio Juruá (MVZ 200907), Barro Vermelho on left bank of Rio Juruá (MVZ 200908), Barro Esperança on right bank of Rio Juruá (MVZ 200909, 200910), Colocação Viravolta on left bank of Rio Juruá (MVZ 200912), Condor on left bank of Rio Juruá (MVZ 200915), Igarapé Nova Empresa on left bank of Rio Juruá (MVZ 200917, 200918), Jainu on right bank of Rio Juruá (MVZ 200927, 200928), Penedo on right bank of Rio Juruá (MVZ 200947), Sacado on right bank of Rio Juruá (MVZ 200934, 200935); *Mato Grosso*, Serra de Chapada (BMNH 3.7.7.67 [holotype of *roberti*]), Serra do Roncador (BMNH 1981.410–1981.417); *Pará*, Santa Rosa on Rio Jamanxim (BMNH 9.3.9.9 [holotype of *tapajinus*]). **Guyana**—*Pomeroon-Supenaam*, Supenaam River

(BMNH 10.5.4.23–10.5.4.28 [type series of *guianae*]), *Potaro-Siparuni*, Iwokrama Forest (ROM 111776), *Upper Takutu-Upper Essequibo*, Gunn's Strip (ROM 106779), Quarter Mile Landing (ROM 98125). **Peru**—*Amazonas*, Huampami on Río Cenepa (MVZ 153528, 155005); *Loreto*, 25 km S Iquitos (TTU 98797), Collpa Salvador on Río Pucacuro (MUSM 17631, 17685), Nina Rumi (MUSM 44981–44984), Ullpayacu on Río Pastaza (MUSM 16424); *Madre de Dios*, 15 km E Puerto Maldonado (KU 144333, 144335, 144336, 144338).

IDENTIFICATION: We recognize *Oecomys roberti* in the broad sense of Carleton and Musser (2015)—including the nominal taxa *tapajinus* Thomas, 1909, and *guianae* Thomas, 1910, as junior synonyms—despite conspicuous geographic variation in ventral pelage coloration and deep phylogeographic structure revealed by mtDNA sequence analyses. This is a moderately large (ca. 45–65 g) species with brownish dorsal fur and a unicolored (all dark) tail that is substantially longer than the combined length of the head and body (LT/HBL = 1.21 ± 0.10) and lacks a terminal pencil of long hairs. Most specimens from south of the Amazon and west of the Rio Tapajós have a continuous streak of self-white ventral fur that extends from chin to anus, but specimens from eastern Amazonia (including those referred by authors to *guianae* and *tapajinus*) have almost completely gray-based ventral fur, as do the specimens we identify as *O. roberti* from the Yavarí-Ucayali interfluve and northern Loreto.

Other morphological traits that we associate with *Oecomys roberti* include 7–9 mm long dorsal fur, short and sparse ungual tufts that do not conceal the claws on digits II–V of the hind feet, shallow zygomatic notches, absence of postorbital processes, incisive foramina that do not extend posteriorly to the level of the M1 alveoli, absence of an alisphenoid strut (in most specimens), a complete stapedial arterial circulation (pattern 1 of Voss, 1988), and a distinctive range of morphometric variation (table 25). Several fluid-preserved specimens had either 17 or 18 caudal scale rows/cm, and a single specimen that

we dissected (AMNH 273112) had small preputial glands that did not extend anteriorly beyond the ventral flexure of the penis. Diploid chromosome counts of $2n = 80$–82 have been reported for specimens of *O. roberti* from central and western Brazil (Amazonas, Mato Grosso, and Rondônia; Patton et al., 2000; Langguth et al., 2005; Suárez-Villota et al., 2018).

Although Rocha et al. (2018) recognized *Oecomys tapajinus* as a valid species, we are not persuaded by their results. Their multigene topology recovered a cluster of four sequences that they identified as *O. tapajinus*, as did separate analyses of two mitochondrial genes (CYTB and COI), but it is not clear whether the nuclear locus they sequenced (intron 7 of beta fibrinogen) supported the same topology when analyzed separately. Because analyses of single-locus data (the mtDNA genome is a single-locus marker) cannot distinguish gene trees from species trees, evidence from other sources—multiple loci, karyotypes, and morphology—is important for confident species delimitation. Unfortunately, the mtDNA clades that Rocha et al. (2018) recovered were not morphometrically distinguishable, karyotypic data were not discussed, and the qualitative character differences that the authors attributed to *roberti* on the one hand and *tapajinus* on the other are inconsistent.[25] Lastly, the application of the name *tapajinus* is problematic because the holotype (BMNH 9.3.9.9) has the ventral coat-color phenotype that Rocha et al. attributed to *roberti* (a continuous midventral streak of self-white fur; Thomas, 1909), the molars are too worn to assess the allegedly diagnostic occlusal morphology of M1, and the type

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[25] *Oecomys roberti* was said to have either an all white venter or to have a continuous midventral streak of self-white fur, but some western Amazonian specimens with the sequence characteristics of *roberti* (see below) have entirely gray-based ventral fur. Similarly, although *tapajinus* usually has entirely gray-based ventral fur, some specimens have a self-white ventral midline (Rocha et al., 2018). We were unable to replicate Rocha et al.'s observations about the dental difference they observed between *roberti* (supposedly without an anteromedian flexus on M1) and *tapajinus* (supposedly with an M1 anteromedian flexus) due to variation and scoring ambiguities in both taxa.

locality (Rocha et al., 2018: fig. 1) is in a region where both *roberti* and *tapajinus* are said to occur and to be difficult to distinguish.

Phylogenetic analysis of sequence data from the western Amazonian material that we identify as *Oecomys roberti* recovered several strongly supported haplogroups (fig. 34). Haplogroup A includes Patton et al.'s (2000) specimens from western Brazil (Amazonas) and a smaller series from southeastern Peru (Madre de Dios); most specimens from this clade have self-white ventral fur, as does the holotype (BMNH 3.7.7.67) and other material we examined from Mato Grosso (but KU 144338 with gray-based buffy ventral fur is an exception). Haplogroup B includes 10 specimens from several localities north of the Amazon, and haplogroup C includes four specimens from the Yavarí-Ucayali interfluve; by contrast with most specimens from haplogroup A, specimens from haplogroups B and C have completely gray-based ventral fur. Average uncorrected pairwise sequence differences at the cytochrome *b* locus (table 26) suggest substantial genetic divergence among these mtDNA clades, but our measurement data document broad morphometric overlap (table 27), and we were unable to discover any phenotypic differences other than the ventral pelage traits described above.

ETHNOBIOLOGY: The Matses do not recognize this species and so have no particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

REMARKS: Of the six specimens collected at Nuevo San Juan, four were taken in seasonally flooded primary forest and two were taken in upland primary forest close to a stream. Four specimens were trapped on lianas 1.0–1.5 m above the ground, one was shot at night on a liana close to the ground, and one was trapped on the ground. Few as they are, these data seem consistent with the observations of other authors (Patton et al., 2000; Rocha et al., 2018) that *Oecomys roberti* (sensu Carleton and Musser, 2015; i.e., including *tapajinus*) is primarily associated with seasonally flooded forests.

## *Oligoryzomys microtis* (Allen, 1916)

Figures 21C, 21F

VOUCHER MATERIAL (*N* = 15): Orosa (AMNH 73833–73846), San Pedro (UF 30473). Additional material that we have not examined was reported from Jenaro Herrera by Pavlinov (1994) and from El Chino by Valqui (2001).

UNVOUCHERED OBSERVATIONS: None.

IDENTIFICATION: The genus *Oligoryzomys* (pygmy rice rats or colilargos) includes numerous species of small, soft-furred, long-tailed oryzomyines that collectively range from Mexico to Tierra del Fuego (Weksler and Bonvicino, 2015b). The western Amazonian species *O. microtis*, one of the smallest cricetids in our region,[26] has short (5–7 mm) grizzled-tawny dorsal fur and gray-based whitish or buffy ventral fur (except on the chin and in the inguinal region, which have self-colored fur). As in most other congeners, the tail is distinctly bicolored, longer than the combined length of the head and body (see below) and lacks a terminal pencil of distinctively long hairs. The hind foot is narrow, and the middle three digits (II, III, and IV) are much longer than the outermost digits (the claw of dI does not extend to the end of the first phalange of dII, and the claw of dV extends only slightly beyond the first phalange of dIV). Cranial characters (also shared with most other congeners) include the absence of supraorbital beading, deep zygomatic notches, large sphenopalatine vacuities flanking the basisphenoid/presphenoid suture in the roof of the mesopterygoid fossa, absence of an alisphenoid strut, and absence of a supraorbital branch of the stapedial artery (carotid circulatory pattern 2 of Voss, 1988).

Most specimens of *Oligoryzomys microtis* from the Yavarí-Ucayali interfluve were collected many years ago, lack external measurements, and have hind feet that are too distorted to measure; therefore, only craniodental measurements are available for comparison with the type series (from the north

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[26] Reliable weight data are unavailable from specimens collected in the Yavarí-Ucayali interfluve, but 10 adults from northern Bolivia (Pando: AMNH 262826–262832, 262837, 262840, 262842) weighed 20 ± 2 g (range: 16–24 g).

0.01 substitutions/site

Brazil: Amazonas (MVZ 200908)
Brazil: Amazonas (MVZ 200928)
92
Brazil: Amazonas (MVZ 200927)
83
Brazil: Amazonas (MVZ 200909)
100
Brazil: Amazonas (MVZ 200907)
Brazil: Amazonas (MVZ 200910)
90
Brazil: Amazonas (MVZ 200912)
74
Brazil: Amazonas (MVZ 200917)
Brazil: Amazonas (MVZ 200918)
100
Brazil: Amazonas (MVZ 200935)
91
Brazil: Amazonas (MVZ 200947)
100
Brazil: Amazonas (MVZ 200915)
100
Brazil: Amazonas (INPA 4193)
Brazil: Amazonas (INPA 4207)
100
100
Peru: Madre de Dios (KU 144333)
97
Peru: Madre de Dios (KU 144335)
Peru: Madre de Dios (KU 144336)
75
100
Peru: Madre de Dios (KU 144338)
Brazil: Amazonas (MVZ 200934)

roberti (A)

92
B

41
Peru: Loreto (MUSM 17631)
Peru: Loreto (MUSM 17685)
Peru: Loreto TTU 98797)
97
Peru: Loreto (MUSM 44981)
Peru: Loreto (MUSM 44984)
100
Peru: Loreto (MUSM 44982)
Peru: Loreto (MUSM 44983)
100
Peru: Amazonas (MVZ 153528)
Peru: Amazonas (MVZ 155005)
100
Peru: Loreto (MUSM 16424)

roberti (B)

99
100
Peru: Loreto (AMNH 273112)*
Peru: Loreto (MUSM 15340)*
97
Peru: Loreto (AMNH 273119)*
Peru: Loreto (AMNH 276701)*

roberti (C)

FIG. 34. Relationships among 33 cytochrome *b* sequences comprising node B (fig. 25), including three haplogroups of *Oecomys roberti* (see text). Asterisks (*) identify sequences from the Yavarí-Ucayali interfluve. Terminals are labelled with country, next-largest administrative unit (state/department/province), and museum catalog number of specimens listed in appendix 3.

bank of the Amazon just upstream from Manaus; Voss et al., 2001: 118–119) and with the series collected by Patton et al. (2000) along the Rio Juruá. Homologous sample means (table 28) from these three series are all within a few tenths of a millimeter of one another, suggesting minimal morphometric divergence. Identical karyotypes from specimens collected at Jenaro Herrera (Sokolov and Malygin, 1994; Aniskin and Volobouev, 1999) and along the Rio Juruá (Patton et al., 2000), together with the results of sequence-based species delimitation analyses (Hurtado and D'Elía, 2019), additionally suggest that pygmy rice rats from the Amazonian lowlands of northeastern Peru are correctly associated with western Brazilian populations previously identified as *O. microtis*.[27]

[27] By contrast, we are not aware of any karyotypic or molecular data that document the occurrence of this species in eastern Amazonia (Weksler and Bonvicino, 2015b: map 232).

TABLE 26

Average Percent Uncorrected Sequence Divergence within and among Western Amazonian Haplogroups of *Oecomys roberti*

	roberti A	*roberti* B	*roberti* C
roberti A	**3.35**		
roberti B	6.93	**0.93**	
roberti C	5.98	4.71	**0.00**

The tail of *Oligoryzomys microtis* is said to be shorter than the combined length of the head-and-body (Allen, 1916; Weksler and Bonvicino, 2015b), which would be a diagnostically useful trait if it were true. However, Voss et al. (2001: 119) expressed doubts about the accuracy of field data associated with Allen's type series; in particular, they pointed out that, although the holotype (AMNH 37091) has measurements suggesting that it had a short tail, several paratypes (AMNH 37088, 37089, 37097) do not. In fact, the variation in relative tail length computed from field measurements of Allen's specimens (LT/HBL = 0.77–1.25) is too large to be credible, so it seems clear that at least some of these specimens were mismeasured. More extensive series of field measurements are now available from Patton et al.'s (2000) large series from the Rio Juruá, in which the mean ratio of tail length to head and body is 1.17.

ETHNOBIOLOGY: This species is not known to the Matses, who have no special name for it.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: No ecological information is available from specimens collected in our region, but along the Rio Juruá this species was usually trapped in grass growing on seasonally exposed river beaches (Patton et al., 2000: 136). At other rainforested sites lacking river beaches, it has been collected only in highly disturbed grass-dominated habitats (e.g., cultivated fields and pastures; Hice and Velazco, 2012). To our knowledge, *Oligoryzomys microtis* has never been trapped in trees.

Scolomys Anthony, 1924

The genus *Scolomys* includes two species of small, short-tailed spiny mice, both of which are endemic to western Amazonia (Gómez-Laverde et al., 2004; Patton, 2015a). Once believed to be allopatric, these species were recently reported to occur sympatrically at several localities in our region by Medina et al. (2015). We have not examined Medina et al.'s specimens (provisionally listed as vouchers, below), but we collected both species at Jenaro Herrera and Nuevo San Juan. Our capture data (summarized below) is consistent with previously reported evidence that these tiny mice are exclusively terrestrial (Patton et al., 2000; Hice and Velazco, 2012), but their diets are completely unknown.

Scolomys melanops Anthony, 1924

Figures 35, 36A

VOUCHER MATERIAL (*N* = 3): Jenaro Herrera (AMNH 276712, MUSM 23822), Nuevo San Juan (MUSM 11223). Additional specimens identified as *Scolomys melanops* that we have not examined were reported by Medina et al. (2015) from Quebrada Betilia (MUSA 15179–15181, 15186), Quebrada Pantaleón (MUSA 15260), and Quebrada Sábalo (MUSA 15204, 15220).

UNVOUCHERED OBSERVATIONS: No observation of this species can be reliably identified as such given the presence of two externally similar congeners in our region (see below).

OTHER SPECIMENS EXAMINED (*N* = 28): **Ecuador**—*Pastaza*, Mera (AMNH 67518, 67520–67523, 67524 [holotype]); *Sucumbíos*, Limoncocha (USNM 513581–513583). **Peru**—*Loreto*, Estación Biológica Allpahuayo (LACM 96052; TTU 85487–85490, 85493–85496, 85499–85502), Km 62–63 on Iquitos-Nauta Highway (TTU 125605, 125607) Mishana on Río Nanay (LACM 97659, 97660), San Jacinto (KU 158212), Teniente López (KU 158213).

IDENTIFICATION: *Scolomys melanops* is easily distinguished morphologically from its sympatric congener *S. ucayalensis* by several qualitative

TABLE 27

External and Craniodental Measurements (mm) and Weights (g) of *Oecomys roberti*

	Haplogroup A[a]	Haplogroup B[b]	Haplogroup C[c]	Combined samples
HBL	129 ± 7 (117–143) 14	129 ± 13 (115–147) 5	123 ± 10 (109–136) 5	128 ± 9
LT	158 ± 10 (141–175) 14	161 ± 14 (143–176) 5	144 ± 12 (135–164) 5	156 ± 12
HF	27 ± 1 (26–29) 15	28 ± 1 (27–29) 5	27 ± 1 (25–29) 6	27 ± 1
Ear	16 ± 1 (15–17) 14	18 ± 2 (15–20) 4	17 ± 1 (16–18) 6	17 ± 1
CIL	29.5 ± 0.8 (28.0–31.2) 15	30.3 ± 1.6 (28.0–31.8) 5	27.9 ± 1.1 (26.4–29.1) 5	29.3 ± 1.3
LD	8.6 ± 0.3 (8.1–9.1) 15	8.9 ± 0.5 (8.3–9.6) 5	8.3 ± 0.4 (7.9–9.0) 6	8.6 ± 0.4
LM	5.0 ± 0.2 (4.8–5.3) 14	4.9 ± 0.1 (4.8–5.1) 7	4.9 ± 0.1 (4.7–5.0) 6	5.0 ± 0.1
BM1	1.4 ± 0.0 (1.3–1.5) 15	1.4 ± 0.0 (1.4–1.5) 7	1.4 ± 0.0 (1.4–1.5) 5	1.4 ± 0.0
LIF	5.2 ± 0.2 (4.9–5.8) 15	5.4 ± 0.4 (5.0–5.8) 5	5.2 ± 0.4 (4.7–5.7) 6	5.2 ± 0.3
BIF	2.6 ± 0.2 (2.0–2.8) 15	2.7 ± 0.2 (2.4–3.0) 5	2.7 ± 0.2 (2.4–2.8) 6	2.6 ± 0.2
BPB	3.3 ± 0.1 (3.1–3.5) 15	3.4 ± 0.2 (3.1–3.8) 5	3.2 ± 0.3 (2.9–3.6) 5	3.3 ± 0.2
BZP	3.0 ± 0.2 (2.8–3.3) 15	3.0 ± 0.2 (2.7–3.4) 6	2.8 ± 0.3 (2.5–3.4) 6	3.0 ± 0.2
LIB	5.5 ± 0.3 (5.0–6.0) 15	5.6 ± 0.4 (5.3–6.2) 5	5.4 ± 0.2 (5.2–5.6) 4	5.5 ± 0.3
ZB	17.3 ± 0.6 (15.8–18.0) 15	17.4 ± 1.1 (15.9–18.7) 5	16.3 ± 0.3 (16.0–16.7) 4	17.2 ± 0.8
LR	10.0 ± 0.4 (9.4–10.8) 14	10.4 ± 0.4 (10.1–10.9) 5	9.4 ± 0.3 (9.1–9.8) 5	10.0 ± 0.5
Weight	57 ± 5 (48–66) 15	62 ± 17 (42–79) 5	54 ± 8 (44–63) 6	57 ± 9

[a] From western Brazil and southeastern Peru. Tabulated statistics include the mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: KU 144333, 144335, 144336, 144338; MVZ 200908–200910, 200912, 200915, 100917, 200918, 200927, 200928, 200934, 200935.

[b] From north of the Amazon in Peru. Tabulated statistics include the mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: MUSM 17685, 44982–44984; MVZ 153528, 155005; TTU 98797.

[c] From the Yavarí-Ucayali interfluve. Tabulated statistics include the mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 268259, 268262, 273112, 273119; MUSM 11215, 15340.

and metrical traits (tables 29, 30). Both species are externally dark gray (almost blackish) as juveniles and subadults, but adult specimens have brownish pelage, and we have not noticed any consistent color contrasts between these species. Instead, the most reliable external difference concerns the length of the fifth digit (dV) of the hind foot: when the digits are straight and undistorted, the claw of dV in *S. melanops* extends to the end of the first phalange of dIV, whereas dV is much shorter (its claw reaching only about half the length of the first phalange of dIV) in *S. ucayalensis*. Based on the few available specimens with intact tails that we were able to examine (both species often suffer partial or complete

loss of this organ), *S. melanops* seems to have a substantially shorter tail in proportion to its head and body (LT/HBL = 0.58 ± 0.09) than does *S. ucayalensis* (0.74 ± 0.02), but sample sizes for both species are small and external measurements are often taken differently by collectors, so it is unwise to place much emphasis on the diagnostic value of this ratio.

By contrast, the skulls of these species are easily distinguished visually, especially by the shorter rostrum, narrower interorbital region, wider zygomatic arches, and more procumbent upper incisors of *Scolomys melanops* by comparison with *S. ucayalensis* (fig. 35). Additionally, the mental foramen of the mandible is often con-

TABLE 28

Measurements (mm) of *Oligoryzomys microtis*

	Type series[a]	Yavarí-Ucayali Interfluve[b]	Rio Juruá[c]
HBL	—	—	88 ± 7 (71–110) 157
LT	—	—	103 ± 7 (80–125) 157
HF	22 ± 1 (20–23) 9	—	23 ± 1 (21–26) 161
Ear	—	—	13 ± 1 (11–15) 161
CIL	20.6 ± 0.3 (20.3–20.8) 4	21.4 ± 0.6 (20.7–21.9) 3	21.2 ± 1.0 (19.1–23.7) 162
LD	5.8 ± 0.2 (5.4–6.1) 7	6.0 ± 0.3 (5.6–6.8) 15	5.9 ± 0.4 (5.2–7.0) 162
LM	3.2 ± 0.1 (3.1–3.4) 6	3.1 ± 0.1 (2.9–3.3) 15	3.2 ± 0.1 (2.9–3.6) 162
BM1	0.9 ± 0.0 (0.9–1.0) 7	0.9 ± 0.0 (0.9–1.0) 15	—
LIF	3.9 ± 0.2 (3.6–4.3) 10	3.9 ± 0.2 (3.4–4.5) 15	4.0 ± 0.2 (3.4–4.7) 162
BIF	1.7 ± 0.1 (1.5–1.8) 10	1.7 ± 0.1 (1.5–1.9) 15	—
BPB	2.1 ± 0.2 (1.9–2.3) 6	2.4 ± 0.2 (2.1–2.7) 15	—
BZP	2.1 ± 0.1 (1.9–2.3) 10	2.2 ± 0.1 (2.0–2.5) 15	2.2 ± 0.2 (1.7–2.8) 162
LIB	3.7 ± 0.2 (3.3–3.9) 9	3.8 ± 0.1 (3.6–4.1) 15	3.8 ± 0.2 (3.3–4.4) 162
ZB	12.2 ± 0.3 (11.7–12.5) 4	12.2 ± 0.4 (11.4–13.1) 11	12.3 ± 0.6 (11.0–13.7) 162
LR	7.1 ± 0.2 (6.7–7.6) 8	7.5 ± 0.4 (7.0–8.5) 14	—

[a] From Manacaparú, Amazonas, Brazil. Tabulated statistics include the mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 37088, 37089, 37091–37097, 37157.

[b] Tabulated statistics include the mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 73833–73846; UF 30473.

[c] Tabulated statistics include the mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for the series measured by Patton et al. (2000), who used the following abbreviations that differ from ours: IOC (for LIB), D (for LD), MTRL (for LM), IFL (for LIF), and ZPL (for BZP). We recomputed descriptive statistics from their raw data, which were kindly provided by J.L. Patton.

cealed from lateral view in *S. melanops*, and the root of the lower incisor usually extends behind the coronoid process (fig. 36A); by contrast, the mental foramen is always laterally exposed and the lower incisor root terminates below the coronoid process in *S. ucayalensis* (fig. 36B). Gómez-Laverde et al. (2004) were not impressed by the species difference in upper-incisor morphology (first remarked by Pacheco, 1991), but the difference is obvious in most of the specimens we examined. Although we did not attempt to measure the angles that define the terminology of rodent incisor procumbency (Thomas, 1919), we agree with Patton and Silva (1995) that the teeth of *S. melanops* seem appropriately described as

proodont, whereas those of *S. ucayalensis* seem appropriately described as orthodont.

We directly compared our Peruvian material of *Scolomys melanops* with Anthony's (1924) type series and other specimens from eastern Ecuador and observed no noteworthy qualitative differences. However, Peruvian specimens have somewhat longer tails and slightly smaller molars than Ecuadorean specimens, differences that we interpret as intraspecific geographic variation. Molecular sequence data would obviously be useful in any future effort to assess the taxonomic status of this species, which is now believed to also vary in karyotypic traits (Moreira et al., 2020).
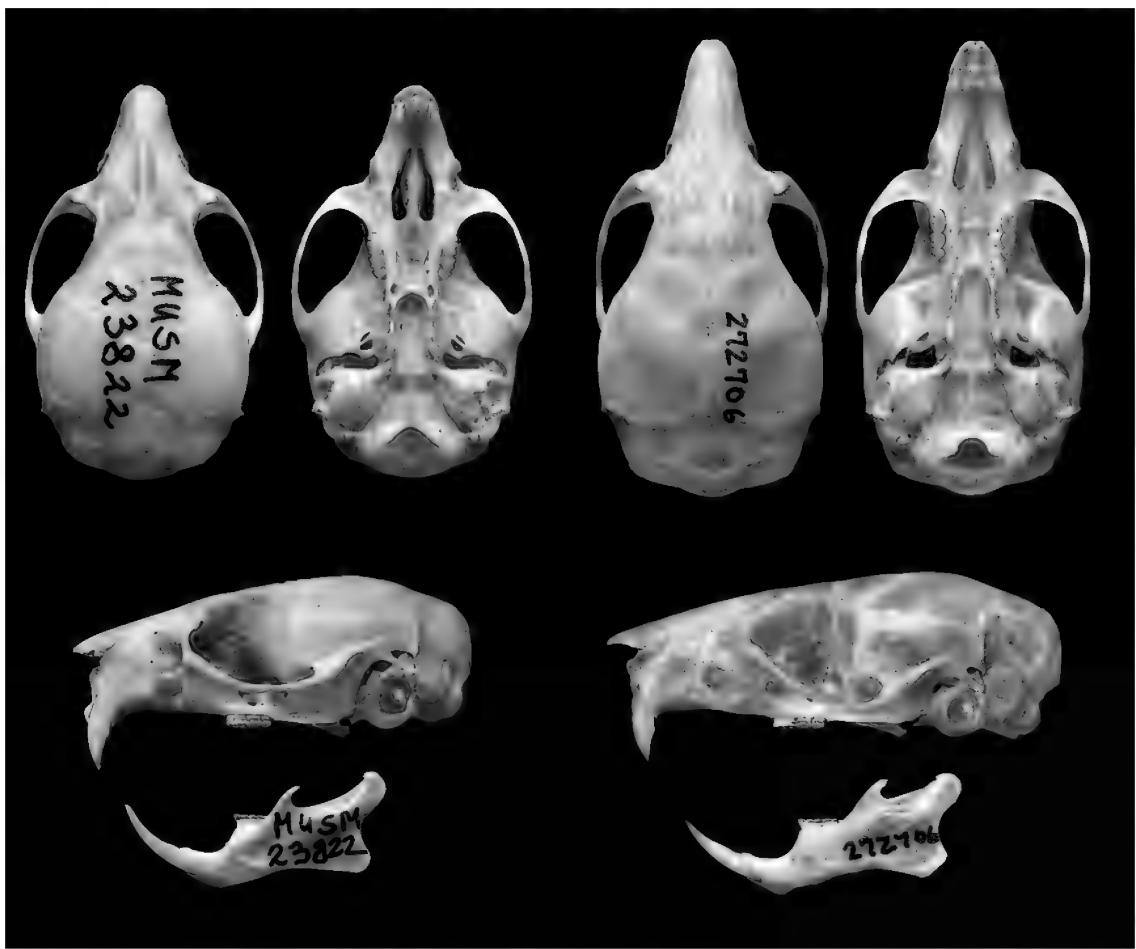
FIG. 35. Dorsal, ventral, and lateral cranial views of *Scolomys melanops* (left, MUSM 23822) and *S. ucayalensis* (right, AMNH 272706). All views about ×2.5.

ETHNOBIOLOGY: The Matses do not recognize this species and have no particular beliefs about it.

MATSES NATURAL HISTORY: The Matses have no definite knowledge of this species.

REMARKS: Of the three specimens of *Scolomys melanops* known from our region, one was trapped on top of a fallen log in well-drained primary forest, one was taken in a pitfall in white-sand forest, and one was taken in a pitfall in swampy primary forest. Although these scant observations are not very informative, they are consistent with capture data from elsewhere that suggest *S. melanops* is a terrestrial species that occurs in multiple primary-forest habitats (Hice and Velazco, 2012: 60).

Scolomys ucayalensis Pacheco, 1991

VOUCHER MATERIAL (*N* = 16): Jenaro Herrera (AMNH 276715; MUSM 5474 [holotype], 23820, 23821), Nuevo San Juan (AMNH 272668, 272686, 272697, 272706, 272708, 272721; MUSM 13356, 13357, 13358, 13359, 13360, 13361). Although we have not examined the specimens that Medina et al. (2015) reported from Quebrada Lobo, Quebrada Betilia, Quebrada Pantaleón, and Quebrada Sábalo,
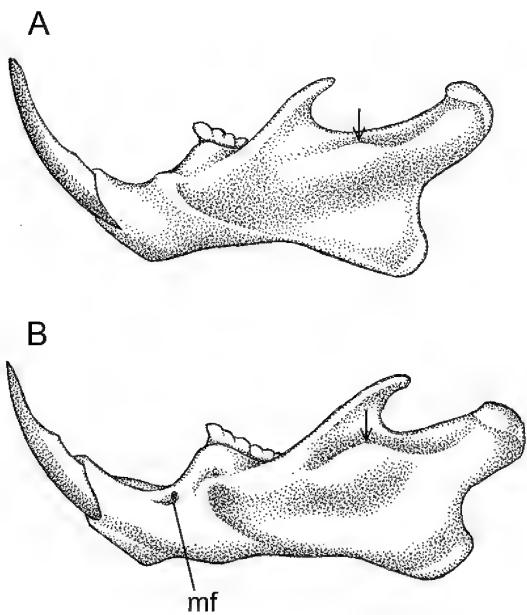
FIG. 36. Lateral mandibular views of *Scolomys melanops* (**A**, MUSM 23822) and *S. ucayalensis* (**B**, MUSM 13360). Vertical arrows indicate the position of the lower incisor root. Note that the mental foramen (**mf**) is laterally exposed in *S. ucayalensis* but it is usually concealed in *S. melanops*.

we assume that they were correctly identified by comparisons with *S. melanops*, which those authors also reported from the latter three sites. Additional material, possibly corresponding to this species, was reported by Valqui (2001) from San Pedro, but we have not seen his specimens.

Unvouchered observations: None.

Identification: The type locality of *Scolomys ucayalensis* is Jenaro Herrera, and neither the topotypic material we examined nor any of our specimens from Nuevo San Juan differ in any essential feature from the subadult holotype. Additionally, our direct comparisons of this Peruvian material with seven paratypes (MVZ 183165–183171) of *S. juruaense* Patton and da Silva, 1995, support the conclusion of Gómez-Laverde et al. (2004) that the latter name is a junior synonym. Diagnostic differences between this species and sympatric *S. melanops* are described in the preceding account.

Although specimens identified as *Scolomys ucayalensis* have been reported from scattered localities north of the Amazon by various authors (e.g., Gómez-Laverde et al., 2004; Brito and Arguero, 2012; Díaz, 2020), we have not personally examined any, and some of these identifications do not seem plausible. For example, the Ecuadorean specimens reported as *S. ucayalensis* by Brito and Arguero (2012) appear to be *S. melanops* based on the accompanying cranial photographs and measurements (especially least interorbital breadth). As mentioned previously, molecular data and karyotypes would provide welcome support for species recognition in future revisionary research with *Scolomys*.

Ethnobiology: The Matses do not recognize this species and so have no particular beliefs about it.

Matses natural history: The Matses have no definite knowledge of this species.

Remarks: Fifteen specimens of *Scolomys ucayalensis* are accompanied by habitat data from our region. Twelve of these (80%) were taken at Nuevo San Juan in Sherman traps set on the ground in a variety of sheltered situations (under fallen trunks, inside hollow logs, beneath leafy understory vegetation, etc.) in well-drained primary forest on hillcrests, on hillsides, and in moist valley bottoms. Two specimens captured in pitfalls at Jenaro Herrera, however, were taken in swampy primary forest and another was taken in a pitfall in secondary vegetation at the same locality. In western Brazil, Patton et al. (2000) captured 23 specimens, all of them on the ground in primary well-drained (terra firme) forest.

Caviomorpha

Caviomorph rodents (the "New World hystricognaths" of authors) are abundantly represented in the Yavarí-Ucayali interfluvial fauna, including members of six ancient clades: Caviidae, Cuniculidae, Dasyproctidae, Dinomyidae, Erethizontidae, and Echimyidae. A key to the caviomorph families is provided in Patton et al. (2015: 689–690), who also provide useful

TABLE 29

Morphological Comparisons between *Scolomys melanops* and *S. ucayalensis*

	S. melanops	*S. ucayalensis*
Claw on digit V of hind foot	extends to end of phalange 1 of digit dIV	extends to about half of phalange 1 of digit IV
Rostral ratio (LR/CIL)	0.31 ± 0.01	0.35 ± 0.01
Zygomatic ratio (ZB/CIL)	0.62 ± 0.01	0.58 ± 0.01
Upper incisors	usually proodont	usually orthodont
Mental foramen	often concealed from lateral view	exposed to lateral view
Lower incisor root	usually extends behind coronoid process	terminates below coronoid process

morphological diagnoses and up-to-date syntheses of the taxonomic literature for caviids, cuniculids, dasyproctids, dinomyids, and erethizontids. By contrast, recent phylogenetic research has transformed our understanding of echimyid systematics, resulting in a substantially revised subfamilial, tribal, and generic taxonomy (see below).

MEASUREMENTS: We measured the following dimensions of caviomorph skulls and teeth (fig. 37):

CIL, condyloincisive length: from the greater curvature of one upper incisor to the articular surface of the occipital condyle on the same side.

LD, length of diastema: from the lesser curvature of an upper incisor to the crown of the anteriormost cheektooth (P4).

MTR, maxillary toothrow length: greatest crown length (except as noted) of the upper cheektooth row (P4–M3).

LIF, length of incisive foramen: greatest anterior-posterior dimension of either the left or right incisive foramen.

BIF, breadth of incisive foramina: greatest transverse dimension across both foramina.

LN, length of nasal: greatest length of one intact nasal bone (left or right).

LIB, least interorbital breadth: the least transverse dimension between the orbits across the frontal bones.

ZL, zygomatic length: distance from the posterior margin of the infraorbital foramen to the posterolateral corner of the zygomatic arch.

ZB, zygomatic breadth: the greatest transverse dimension across the zygomatic arches.

AGE DETERMINATION: Most caviomorph rodents exhibit premolar replacement, shedding their deciduous teeth (dP4/dp4) as their permanent premolars erupt. As defined herein, non-echimyid caviomorphs with incompletely erupted molar dentitions are juveniles, those with dP4—M3 are subadults, and those with completely erupted permanent maxillary dentitions (P4–M3) are adults. Echimyids, however, do not replace dP4 and conspecific individuals with completely erupted toothrows exhibit substantial ontogenetic size variation. Age determination in echimyids is discussed in the account for that family (below).

Caviidae

Hydrochoerus hydrochaeris (Linnaeus, 1766)

Figure 38

VOUCHER MATERIAL (*N* = 5): Boca Río Yaquerana (FMNH 88900), Nuevo San Juan (AMNH 268264, MUSM 11226–11228 [not seen]).

UNVOUCHERED OBSERVATIONS: Jenaro Herrera (Ríos et al., 1974; Tovar, 2011), Río Yavarí (Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), San Pedro (Valqui, 1999, 2001).

IDENTIFICATION: *Hydrochoerus hydrochaeris* is the only currently recognized capybara spe-

TABLE 30

External and Craniodental Measurements (mm) and Weights (g) of
Scolomys melanops **and** *S. ucayalensis* **from Peru**

	S. melanops				S. ucayalensis[b]
		Yavarí-Ucayali			
	North Loreto[a]	AMNH 276712	MUSM 238922	MUSM 11223	
HBL	96 ± 6 (90–105) 5	—	89	86	95 ± 4 (91–99) 4
LT	56 ± 10 (43–69) 5	—	80	70	70 ± 1 (69–72) 4
HF	20 ± 1 (19–22) 10	22	22	20	21 ± 1 (20–22) 9
Ear	15 ± 1 (14–16) 10	15	15	16	16 ± 1 (15–18) 9
CIL	20.4 ± 0.9 (18.9–21.8) 17	19.4	19.4	19.3	21.2 ± 0.6 (20.2–22.1) 9
LD	6.1 ± 0.3 (5.5–6.6) 17	6.1	6.0	5.9	6.4 ± 0.4 (6.0–7.1) 9
LM	2.5 ± 0.1 (2.3–2.7) 17	2.4	2.4	2.4	2.7 ± 0.1 (2.6–3.0) 13
BM1	0.8 ± 0.0 (0.7–0.8) 17	0.8	0.8	0.8	0.9 ± 0.0 (0.8–0.9) 13
LIF	3.9 ± 0.2 (3.6–4.3) 17	3.7	3.8	4.0	4.0 ± 0.2 (3.7–4.3) 9
BIF	2.5 ± 0.2 (2.1–2.9) 16	2.0	2.2	2.1	2.2 ± 0.1 (2.0–2.4) 9
BPB	3.0 ± 0.2 (2.7–3.5) 17	2.9	3.1	2.6	2.9 ± 0.1 (2.8–3.2) 9
BZP	1.6 ± 0.2 (1.2–1.9) 17	1.6	1.4	1.6	1.8 ± 0.1 (1.6–1.9) 9
LIB	5.2 ± 0.2 (4.8–5.7) 17	4.8	5.1	5.0	5.8 ± 0.2 (5.6–6.0) 9
ZB	12.6 ± 0.5 (11.7–13.5) 16	12.3	12.5	12.1	12.3 ± 0.3 (11.9–12.7) 8
LR	6.4 ± 0.3 (6.0–7.1) 16	6.0	6.1	6.2	7.5 ± 0.3 (6.9–7.9) 9
BR	5.0 ± 0.3 (4.6–5.4) 10	—	4.8	—	4.9 ± 0.1 (4.7–5.0) 9
Weight	26 ± 5 (20–37) 10	28	30	21	30 ± 3 (26–37) 9

[a] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: KU 158212, 158213; LACM 96052, 97659, 97660; TTU 85487–85490, 85493–85496, 85499–85502, 125605, 125607.

[b] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 272668, 272686, 272706, 272708, 272721, 276715; MUSM 5474 [holotype], 13356, 13357, 13359, 13360, 23820, 23821.

cies in Amazonia. The two adult specimens we examined from the Yavarí-Ucayali interfluve (table 31) have measurements that fall within the range of morphometric variation previously documented in the literature (e.g., Husson, 1978; Mones and Ojasti, 1986), and their crania agree in all qualitative respects with published descriptions of the species (Husson, 1978; Dunnum, 2015).

ETHNOBIOLOGY: The Matses name for the capybara is memupaid, which is not linguistically analyzable. No subtypes are recognized by the Matses.

The Matses do not eat or kill capybaras, which sometimes enter swiddens to eat crops, but too infrequently for them to be considered pests.

Prior to peaceful contact, the Matses avoided rivers and navigable streams, so they seldom encountered capybaras. As is the case with most infrequently encountered animals, the Matses consider capybaras to be dangerous because they can make children ill if a parent kills or even looks at one.

MATSES NATURAL HISTORY: The capybara's head and teeth are similar to those of the paca, but larger. It is reddish. Its tracks are similar to
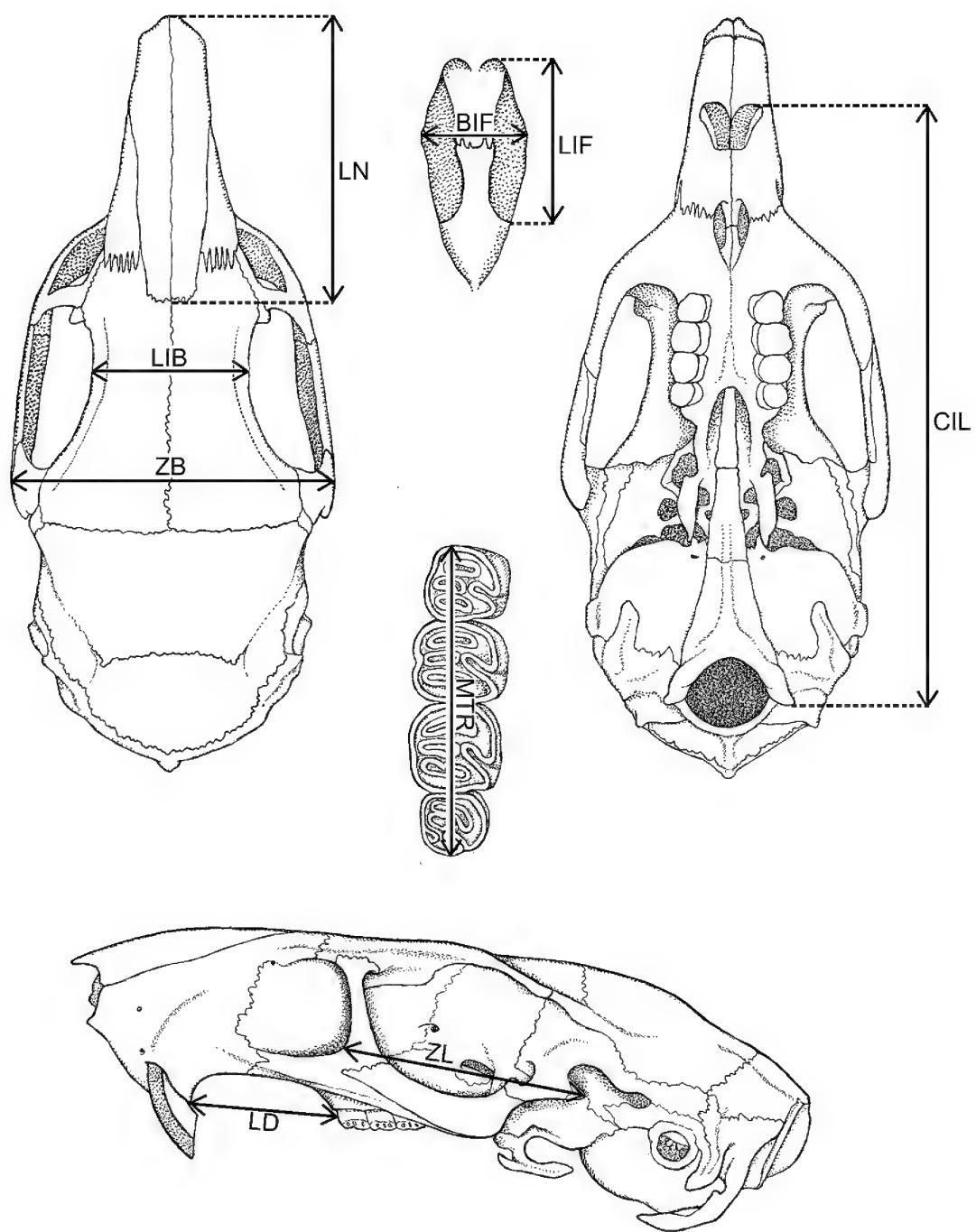
FIG. 37. Limits of nine caviomorph craniodental measurements defined in the text.
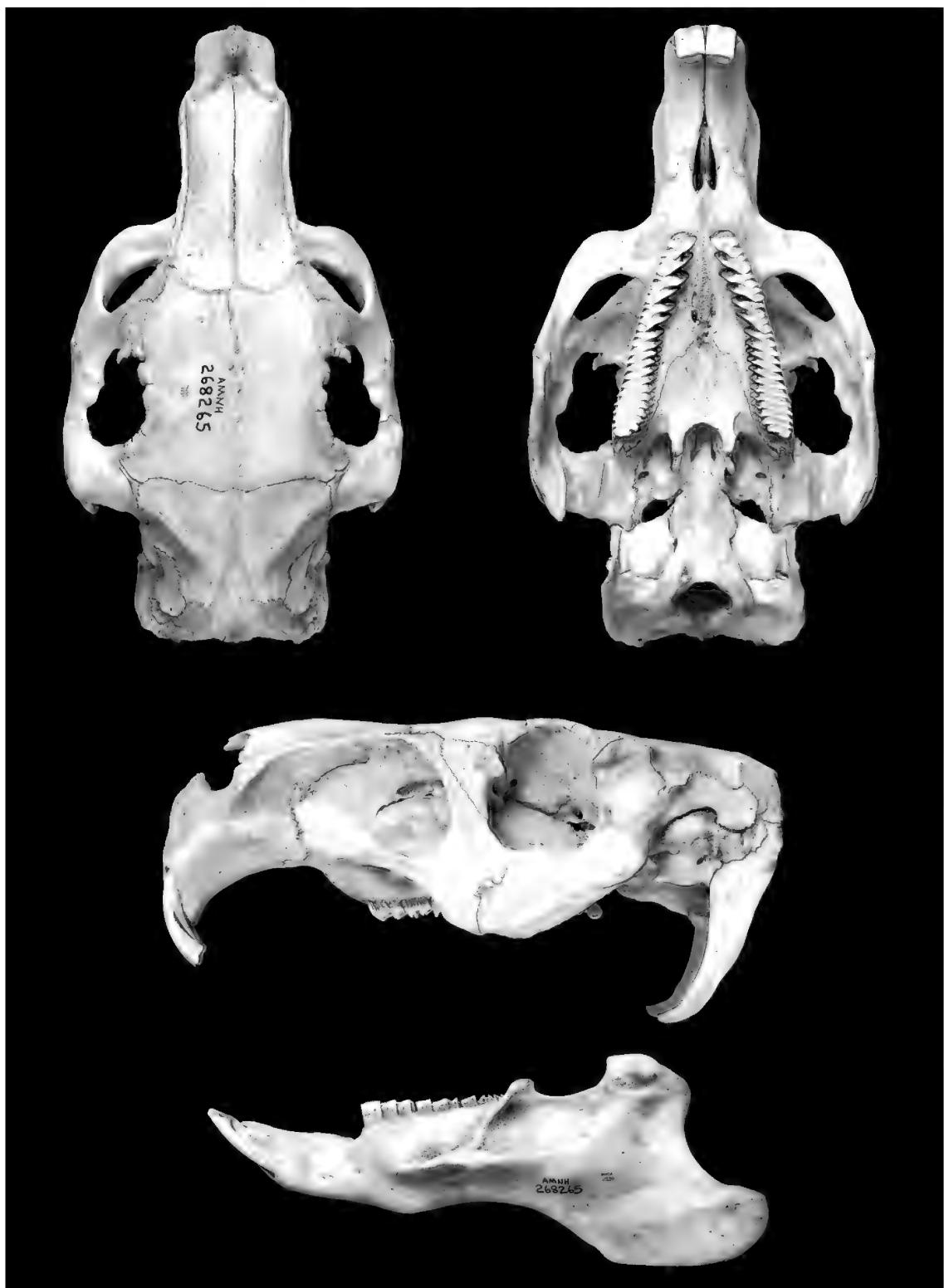
a young tapir's tracks. Its feet are webbed. It defecates in a pile, and its feces resemble seeds of the <u>tedia</u> tree (*Minquartia guianensis* [Olacaceae]).

Capybaras spend most of their time along rivers. They also go into upland forest to forage, but they do not lie down there. They infrequently come to swiddens to eat plantains. Many capybara tracks can be observed along rivers.

Capybaras do not make nests.

Capybaras are mostly nocturnal. They follow rivers as they forage. They stop to rest during the night lying down as a group in open-canopied forest along a river, under a blowdown, or in the floodplain of a large stream. To sleep they do likewise. They can swim and cross rivers, and they can swim underwater.

Capybaras live in herds, although sometimes a single animal travels alone. Sometimes there are only two or three.

Capybaras are preyed upon by jaguars, black caimans, and anacondas. They plunge into the river when they see a jaguar or a human. Many flies buzz around capybaras.

Capybaras make vocalizations that sound like the breaking of a dry stick. They grunt saying "os os os os" as they plunge into the water when they see a person.

Capybaras eat grass that grows along rivers during the dry season, young leaves of <u>buku</u> trees (*Cecropia* spp.), leaves of arrow canes (*Gynerium sagittatum* [Graminae]), and new leaves of the <u>akte pinchuk</u> palm (*Astrocaryum jauari*). In Matses swiddens they eat the leaves and stems of sugar cane and the leaves of plantain and banana plants. They do not eat fruits.

REMARKS: Of the two specimens of *Hydrochoerus hydrochaeris* accompanied by habitat information from our region, one (an adult female, one of a group of four individuals) was shot in the late afternoon on a beach of the Río Gálvez. The second specimen (an adult male, possibly solitary) was shot at night on the edge of a wide (10 m) stream bordered by primary upland forest.

The Matses do not have much to say about capybara natural history, but their sparse remarks are of some interest because most fieldwork on this species (e.g., the studies reviewed by Mones and Ojasti, 1986) has been carried out in savanna landscapes. Matses observations about capybaras broadly resemble those of Soini and Soini (1992), whose research was based in the Pacaya-Samiria reserve (close to the Yavarí-Ucayali interfluve in southern Loreto department), but those authors report that capybaras are active both by day and by night. Because the Matses were unfamiliar with capybaras until recently and do not hunt them, Soini and Soini's attribution of cathemeral (rather than primarily nocturnal) activity to these rodents seems more plausible.

Cuniculidae

Cuniculus paca (Linnaeus, 1766)

Figure 39

VOUCHER MATERIAL (*N* = 3): Nuevo San Juan (MUSM 11238), Quebrada Esperanza (FMNH 88899), Santa Cecilia (FMNH 86922). Additionally, Pavlinov (1994) reported four ZMMU specimens from Jenaro Herrera that we have not seen.

UNVOUCHERED OBSERVATIONS: Actiamë (Amanzo, 2006), Divisor (Jorge and Velazco, 2006), Itia Tëbu (Amanzo, 2006), Jenaro Herrera (Ríos et al., 1974; Tovar, 2011), Río Yavarí (Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), Tapiche (Jorge and Velazco, 2006), San Pedro (Valqui, 1999, 2001).

IDENTIFICATION: Like the capybara (see above), *Cuniculus paca* (formerly *Agouti paca*; Patton, 2015b) is a widespread, monotypic, and morphologically unmistakable species. Most cranial measurements of our single adult voucher (table 31) are within the range of morphometric variation among topotypical (northeastern Ama-

FIG. 38. Dorsal, ventral, and lateral cranial views of *Hydrochoerus hydrochaeris* (AMNH 268265). All views about ×0.4.

TABLE 31

Measurements (mm) and Weights (g) of *Hydrochoerus hydrochaeris* and *Cuniculus paca* from the Yavarí-Ucayali Interfluve

	H. hydrochaeris		*C. paca*	
	AMNH 268264♂	FMNH 88900♀	FMNH 86922♀	FMNH 88899♂
Age	adult	adult	subadult[a]	adult
HBL	1096	820	680	958[b]
LT	19	—	—	7
HF	243	195	115	120
Ear	68	58	44	45
CIL	226.0	160.0	123.5	135.7
LD	67.7[c]	44.3[c]	43.1	50.8
MTR	81.8[c]	60.9[c]	30.1	30.6
LIF	18.6	14.2	—	—
BIF	9.6	7.4	—	—
LN	84.6	—	48.1	45.6
LIB	66.6	45.0	37.6	40.7
ZL	80.4	51.7	54.4	76.1
ZB	133.9	96.3	81.8	108.4
Weight	48,500	—	—	—

[a] With fully erupted P4s, but retaining fragments of both dp4s, which are in the process of being replaced. Unlike the rugose dorsolateral cranial surfaces of fully adult individuals, the skull of this specimen is mostly smooth.
[b] Possibly inaccurate (see text).
[c] Alveolar measurements.

zonian) specimens previously reported by Voss et al. (2001: 152) and Husson (1978: table 84), but the head-and-body length that we computed from measurements recorded by the collector (958 mm) is substantially larger than any previously reported values for this dimension (600–800 mm; Pérez, 1992).

ETHNOBIOLOGY: The principal Matses name for the lowland paca is tambis. In closely related Panoan languages, the name for the paca is mapua, and in most other Panoan languages it is anu, suggesting that the Matses term tambis is a relatively new coinage, probably invented in response to word taboo (Fleck and Voss, 2006). Two possible etymologies have been suggested by the Matses: tan- ("cheek") + bis ("rough," in reference to its corrugated cheekbone); and taë ("foot") + an- ("sole") + bis ("rough," in reference

to the rough soles of their feet). Tambis has three archaic synonyms: made (the usual term for *Dasyprocta* spp. in other Panoan languages), mapua, and tampodo (the latter two of unclear etymology). In the language used in the Matses' komok ceremony (Romanoff et al., 2004), the paca and the agouti are called ana pachi, which means "soft mouth" or "soft tongue."

Three subtypes of the paca are recognized by Matses hunters: tambis çhëşhë ("dark-colored paca"), tambis uşhu ("light-colored paca"), and tambis piu ("reddish paca"). The dark variety is said to be the largest of the three and the red variety the smallest. The pacarana (*Dinomys branickii*) is called tambisbiekkid ("one that is like a paca"), and spiny rats (*Proechemys* spp.) are called tambisëmpi ("little pacas"), but these are clearly not considered subtypes of the paca.
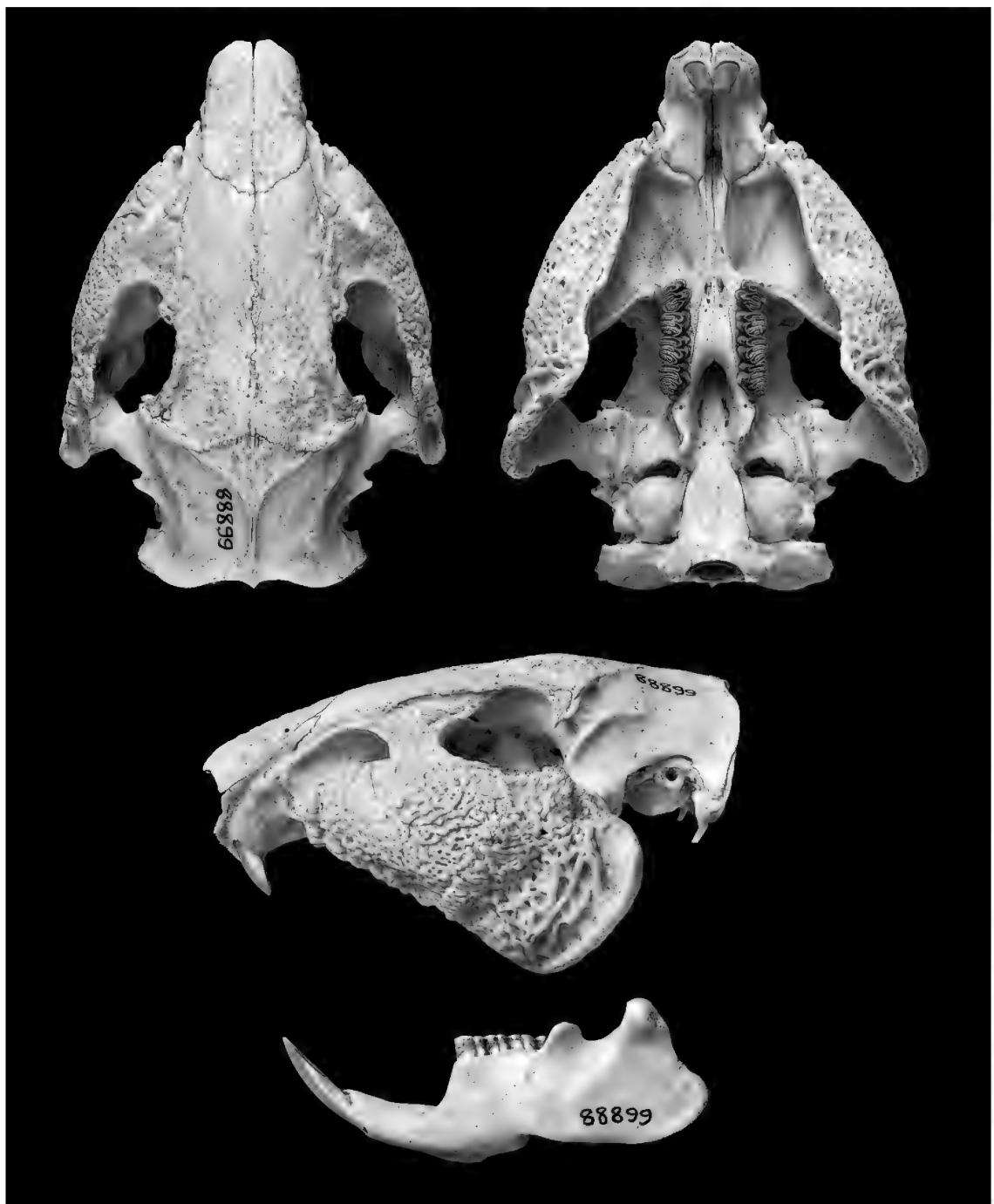
FIG. 39. Dorsal, ventral, and lateral cranial views of *Cuniculus paca* (FMNH 88899). All views about ×0.6.

FIG. 40. Lower incisor of a paca bound to a palm-wood shaft for use as an arrow sharpener (photo by D.W.F.).

The paca is one of the most commonly killed game species. The traditional, and still most frequently practiced method for hunting pacas is to search for their burrows with dogs during the daytime. While a single hunter and his dog (or dogs) may successfully kill a paca this way, a paca hunter will typically be aided by his wife (or wives), grown children, and perhaps a second hunter. Such hunts are always along streams, and only when the streams are not flooded, which can be any time of the year, but more commonly during the dry season. Typically, a hunter observes fresh paca tracks along a stream while hunting other game, and the following day organizes a paca hunt. The hunting party searches for additional tracks along the stream, working their way downstream along both banks. Dogs are also placed on both banks, with the hunters guiding them as the dogs search for burrows. In places where there are many tracks, the hunters make the dogs search more carefully, whereas the dogs

advance faster along stretches of the stream where there are no tracks. As paca burrows tend to have multiple entrances, and pacas sleep in different burrows each night, the dogs do a lot of sniffing and listening when they find a burrow to determine whether it is inhabited. If dogs find an inhabited burrow, they will poke their noses into the different burrow openings, and the paca will eventually spring out of one of them. The dogs then give chase, barking all the while, with the hunters rushing after them. The fleeing paca may run downstream or leave the floodplain to cross over a ridge to a larger stream.

To escape pursuing dogs, the paca frequently plunges into a deep bend of the stream and stays submerged, holding its breath. The dogs reach the streambank and bark. When the hunters catch up and see that the water is murky, they know the paca is submerged somewhere in the deep part of the stream. The hunters then pile logs upstream and downstream from the deep part, blocking the

stream at the points where the paca could escape by swimming underwater. A male hunter then sharpens a pole cut from a sapling or small palm tree to make a spear. The lead hunter cuts an L- or J-shaped length of liana to probe along the bank for any underwater cavities where the paca might be hiding. Meanwhile, the other hunters stand ready to block the paca from escaping. When the paca is touched with the liana-stem probe, it emerges from the cavity or from the bottom of the stream, and one of the hunters stabs it as it tries to escape. Although women and children do not spear pacas, they help urge the dogs, search for tracks, block the stream with dead logs, etc. If the hunting party is lucky, they may kill two or more pacas in a single day.

When pursued by dogs, rather than going into a stream, the paca sometimes enters a hole in the ground or a hollow log. If the hole is not deep, the hunter will sharpen a stick or the stem of an oninan siante palm (*Iriartella stenocarpa*, the Matses name literally means "giant otter's spear") and stab it. If the hole is too deep and he cannot kill it by that method, he will block the entrance hole, make a small opening in the log or in the roof of the burrow, introduce a noose tied to a stick, wait for the paca to approach the opening, and then strangle it (the same method is used for killing collared peccaries that have taken refuge in hollow logs; Voss and Fleck, 2017).

Other methods for hunting pacas require a flashlight and a shotgun, which the Matses did not have regular access to until the 1980s. As a result, few Matses are experienced night hunters. There are three night-hunting methods currently employed by the Matses: (1) hunting from a boat, (2) waiting in ambush on a stream bank, and (3) hunting while walking along a trail. The first two methods are only used in the dry season, when pacas regularly come to large streams to drink because smaller streams are dry.

To hunt from a boat or canoe at night, the hunter travels upstream during the afternoon and paddles quietly downstream after dark, illuminating the banks for pacas that have come down to drink, usually several hours after dusk.

Caimans and tapirs may also be killed while hunting pacas from boats.

A paca can be ambushed at night if its path to a stream has been discovered by day. The hunter goes to the place at dusk, sits on the opposite bank, and listens for the paca. When he hears it lapping water, he shines his flashlight on it (holding the flashlight and the barrel of the gun in the same hand) and shoots. The paca usually freezes in the beam of the light if the hunter is sufficiently quiet.

Hunting pacas while walking on a trail at night is often motivated by having found a tree with ripe fruits on the ground and evidence that a paca has been feeding there. Since most trees fruit between December and May, this hunting strategy is mainly used in the rainy season, and because one does not travel far while hunting at night, most pacas killed in this way are taken in secondary forest or abandoned swiddens. Nine-banded armadillos are also commonly killed during these hunts, and sometimes also deer.

Pacas are cooked by boiling, after singeing and scraping off the fur. The skin, which is very soft when boiled, the underlying fat, and the tender flesh are much esteemed by the Matses. Excess paca meat is sometimes smoked (for example, when more than one paca is killed on a hunt), but smoked paca meat spoils more quickly than other, tougher meat. The lower incisors of female pacas are used to make arrow sharpeners (fig. 40). Pacas are sometimes kept as pets when they are young. In addition to being a primary game species, pacas are pests that enter Matses swiddens at night to eat manioc tubers.

Pregnant women do not eat young pacas, lest they grow weak while giving birth. Young men do not eat young pacas lest they freeze with fear when they see a jaguar. Everyone, however, may eat adult pacas.

MATSES NATURAL HISTORY: The paca has longitudinal stripes along its body, both as adults and as newborns. It has sharp, paired incisors on the top and bottom of its mouth. It has whiskers on its snout that move as it sniffs. The soles of its feet are rough. It has a tiny stump for a tail.

FIG. 41. Snail shells said to have been piled on the bank of a small stream by a paca. (Photo by D.W.F.).

The paca usually dens and forages near streams. It also forages for dicot tree fruits in upland forest, and feeds on swamp-palm (*Mauritia flexuosa*) fruits in palm swamps. Pacas are common in primary forest and, especially, in secondary forest.

The paca lives in burrows in the ground or in hollow logs. Each paca uses multiple dens or burrows, and it sleeps in a different one each night. A paca burrow has multiple entrances, which the paca covers with dry leaves when it is occupied. Burrows are often near streams, often right on the bank, but pacas also have burrows in headwater gullies, typically in thickly vegetated areas, which they use when streams are flooded. The area around a den where a female is suckling its young is muddy with many tracks. All paca burrows have tracks around the entrances. The sleeping chamber is larger than the burrow entrances.

The paca is nocturnal. It sets out in the early evening (about half an hour after nightfall) and starts following a stream. As the paca forages, it follows its path, which is mostly in upland forest. From its path it descends to a waterway to forage for aquatic snails, or to a palm swamp to eat swamp-palm (*Mauritia flexuosa*) fruits; then it forages for fruits in upland forest, then descends to a waterway again to forage again for snails, and so on throughout the night, traveling very far. During the dry season, it travels to a river or large stream to drink water around 20:00. When it eats fruits, seeds, or palm nuts, it gathers these items at one place near the base of the tree from which they fell, leaving a pile of remains in one place. It eats mud at mineral licks, although not as often as tapirs and deer do. While foraging, the paca may stop at one of its burrows, but it does not stay to sleep there if it is still early. Just

FIG. 42. Close-up of a snail said to have been eaten by a paca. (Photo by D.W.F.)

before dawn it seeks out its nearest burrow and enters it right at dawn. It sleeps lying on its side.

Males and females do not live or travel together. They copulate when they encounter each other while foraging, making grunting noises ("oo oo"), and then they go their separate ways. The paca gives birth to one young during the rainy season in a burrow that it fills completely with leaf litter. It lies with its young in its burrow during the day and goes out to feed at night, leaving the young in the nest. When the young paca is old enough to walk, the mother begins to use other burrows and, once her offspring is weaned, she begins taking it with her to forage. Once the young paca is strong, it leaves its mother.

Pacas are preyed upon by jaguars, pumas, ocelots, margays, short-eared dogs, bush dogs, and anacondas. They have many chiggers on their cheeks. During the dry season they are infested with botfly larvae.

Pacas call out saying "tëkëdës" and "os os os."

Pacas eat many types of dicot tree fruits, especially those of kuëte mëdiad (an unidentified tree with starchy fruits that the Matses cook before eating). It also likes sweet fruits, including those of bata (*Pseudolmedia* spp, or *Perebea* spp. [Moraceae]), këku (*Parahancornia peruviana* [Apocynaceae]), and machiste (*Couepia* spp. [Chrysobalanaceae]). It eats the seeds of some dicot tree fruits, including those of tote (*Eschweilera* spp. or *Lecythis* spp. [Lecythidaceae]). Pacas also eat the endosperm of shuinte mapi palm (*Attalea tessmanii*) nuts after gnawing at the husk. They also

eat the mesocarp of swamp-palm (*Mauritia flexuosa*) fruits.

The paca often eats aquatic snails by searching for them while wading in small streams or shallow stretches of larger streams. The snails are found on the underside of submerged leaves or on rotten logs at the curves of the streams (where water does not flow much). The paca takes them onto the bank to eat them and leaves a pile of snail shells where it has eaten them. At the same streams where it eats aquatic snails it also eats crabs. It forages for snails at various streams in one night, following streams and crossing to other streams searching for snails.

Pacas eat manioc that the Matses plant in their swiddens by scraping away the dirt and eating the tuber. It does not kill the manioc plant by gnawing through the stem (unlike the pacarana, which is more destructive in this respect). It also eats plantains when a plantain plant falls over.

The paca eats rotten meat, such as parts of kills that have been stashed by a jaguar or puma, and it eats a type of white fungus that grows on the side of rotten logs.

REMARKS: The single paca specimen accompanied by habitat data from our region was speared in the daytime by a Matses man hunting with dogs in primary upland forest.

The Matses have a lot to say about pacas, most of which agrees with, or plausibly complements, published research reports (e.g., Collett, 1981; Pérez, 1992; Dubost and Henry, 2006). The single striking exception is the Matses claim that pacas routinely eat aquatic snails, for which we could find no corroborating datum in the scientific literature. All the Matses we spoke with, however—hunters and women alike—insist on this and showed us piles of broken shells near streams as evidence (figs. 41, 42). Because the Matses are seldom mistaken about the habits of primary game species (Voss and Fleck, 2011; Fleck and Voss, 2016), future dietary studies of pacas should be alert for the presence of snail shell fragments, radulas, or DNA in stomach contents or scat.

Dasyproctidae

Dasyproctids include two genera of large, diurnal, terrestrial frugivorous/granivorous rodents: agoutis (*Dasyprocta*) and acouchies (*Myoprocta*). Whereas agoutis are found in rainforest and dry forests from Mexico to northern Argentina, acouchies are only found in Amazonian rainforest. Apparently, no more than one species of each genus is found in any local Amazonian fauna, and the Yavarí-Ucayali interfluve is no exception.

Dasyprocta fuliginosa Wagler, 1832

Figure 43

VOUCHER MATERIAL (*N* = 8): Boca Río Yaquerana (FMNH 88901, 88902), Nuevo San Juan (AMNH 268266; MUSM 11232), Quebrada Esperanza (FMNH 88903–88906). Additionally, Pavlinov (1994) reported a ZMMU specimen (identified as "*Dasyprocta aguti*") from Jenaro Herrera that we have not seen.

UNVOUCHERED OBSERVATIONS: Actiamë (Amanzo, 2006), Choncó (Amanzo, 2006), Divisor (Jorge and Velazco, 2006), Itia Tëbu (Amanzo, 2006), Jenaro Herrera (Ríos et al., 1974; Tovar, 2011; Gorchov et al., 2004), Río Yavarí (Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), San Pedro (Valqui, 1999, 2001), Tapiche (Jorge and Velazco, 2006), Wiswincho (Escobedo-Torres, 2015).

IDENTIFICATION: *Dasyprocta fuliginosa*, commonly known as the black agouti, is a distinctively large species with blackish fur that is finely grizzled with white- or gray-tipped hairs. Skins from our region conform closely to the pelage description in Patton and Emmons (2015a), but the rump hairs are very long (forming an overhanging fringe) and are streaked with white (the individual hairs having long white tips), resembling the phenotype those authors attributed to southern Venezuelan specimens.

According to the most recent authoritative review of agouti taxonomy (Patton and Emmons,

2015a), the genus *Dasyprocta* includes 10 South American species, all of which are allopatric and distinguishable primarily by pelage coloration; apparently, all agoutis have the same karyotype ($2n = 64$, FN = 122 or 124), and although size differences are sometimes cited in support of taxonomic assignments, morphometric data are seldom analyzed (or even tabulated). As recognized by Patton and Emmons (2015a), *D. fuliginosa* is monotypic, occurs throughout most of western Amazonia, and includes several nominal species as subjective junior synonyms: *nigra* Gray, 1842; *nigricans* Wagner, 1842; *zamorae* Allen, 1915b; *mesatia* Cabrera, 1917; and *apurensis* Delacour, 1922. Recently reported results from molecular sequence analyses, however, are strikingly inconsistent with the current classification of agoutis.

Ruiz-García et al. (2022) analyzed complete mitochondrial genomes from 93 specimens of *Dasyprocta* that the authors identified to species a priori based on pelage coloration and geography. Their phylogenetic results suggest that the *D. fuliginosa* phenotype is shared by several lineages that do not comprise a monophyletic group: one ("Fuliginosa 3") was embedded within a predominantly transAndean clade that included specimens of *D. punctata* Gray, 1842, whereas another ("Fuliginosa 4") was recovered as the sister clade of *D. punctata* (including "Fuliginosa 3") + *D. leporina* (Linnaeus, 1758). Most sequenced specimens phenotypically identified as *D. fuliginosa*, however, together with a few identified as *D. kalinowskii* Thomas, 1897, were recovered as the sister taxon of *D. azarae* Lichtenstein, 1823.

Although some of these relationships were not strongly supported, Ruiz-García et al.'s (2022) results, taken at face value, clearly signal the need for a comprehensive revision of agouti taxonomy. As discussed by the authors, either hybridization followed by mitochondrial introgression or widespread homoplasy in coat-color evolution might explain the observed discrepancies between pelage phenotypes and mtDNA lineages. Both alternatives

are taxonomically problematic, but neither can be evaluated at present.[28]

An additional, related difficulty concerns the unknown type locality of *Dasyprocta fuliginosa*, "Brasilia versus flumen Amazonum" (Wagler, 1832: 1221). According to Allen (1915b), the type might have been collected at or near Borba (on the lower Rio Madeira), but there is no way to be sure and the specimen itself is apparently lost. (Although Wagler said that the type was in Munich, it cannot now be found at the ZSM [A. van Heteren, personal commun.].) On the assumption that it was collected in western Brazil, however, then this name could apply either to the haplogroup that Ruiz-García et al. (2022) called "Fuliginosa 4" or to "Fuliginosa 1," both of which included western Brazilian sequences. Ruiz-García et al. (2022) did not sequence any specimens from the Yavarí-Ucayali interfluve, but one sequence from nearby Pucallpa (fig. 1) was recovered in "Fuliginosa 1," so our material might belong to that lineage.

ETHNOBIOLOGY: The principal name for the black agouti is mëkueste, which can be analyzed as composed of the prefix më- ("hand, forearm, forefoot") and kueste ("stick"), presumably in reference to its thin front legs. The name for the agouti in most Panoan languages is made or mari, so it is likely that the term mëkueste is a recent coinage, probably in response to word taboo (Fleck and Voss, 2006). It has one archaic synonym, tsikudu, which can be translated as "gray rump." In the language used in the Matses' komok ceremony (Romanoff et al., 2004), the agouti and the paca are called ana pachi, which means "soft mouth" or "soft tongue." Two subtypes of agoutis are recognized by Matses hunters: mëkuestedapa ("large agouti") and mëntsod (meaning unknown).

The agouti is a primary game species for the Matses. Although agouti meat is not as

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[28] No nuclear loci were sequenced by Ruiz-García et al. (2022), and the correspondence (or lack thereof) between coat-color phenotypes and clade membership cannot be critically assessed because tissues were obtained from roadkill or bushmeat rather than from museum specimens.
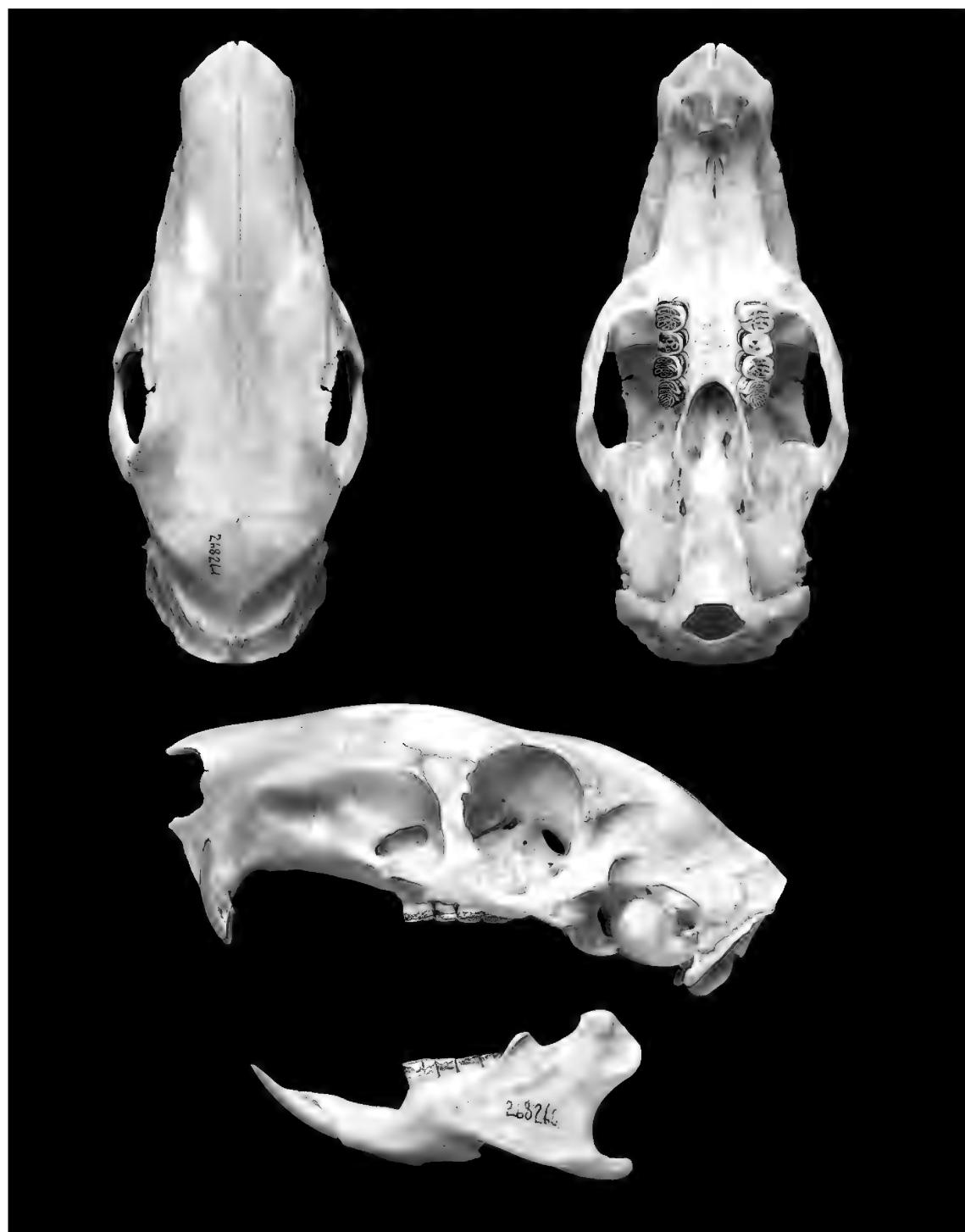
FIG. 43. Dorsal, ventral, and lateral cranial views of *Dasyprocta fuliginosa* (AMNH 268266). All views about ×0.8.

esteemed as paca meat, agoutis are often killed because they are the principal pest of Matses swiddens. In fact, the term m<u>ë</u>kueste is used to refer to human thieves, and the term <u>ampe</u> ("thief") is often used to refer to the agouti (although it is more of a nickname than a real synonym). When it is discovered that an agouti has been eating manioc in a swidden, a hunter will go to his swidden and wait with a shotgun (formerly with bow and arrow) at the place where the agouti had fed on manioc the previous day. Agoutis usually come to swiddens at dawn or in the late afternoon (around 17:00), so that is when a hunter will wait to kill them.

Agoutis are also killed when they are encountered by hunting dogs as the agouti is foraging or feeding in the forest. The dogs chase the agouti until it finds refuge in a burrow or hollow log. When the hunter catches up, he blocks any possible exits with dry or rotten wood, makes a noose from epiphyte stems attached to a short stick, pokes a small hole in the roof of the burrow or hollow log, introduces the noose, and strangles the agouti (the same technique is used for collared peccaries; Voss and Fleck, 2017). If the hunter is not accompanied by hunting dogs, he may shoot an agouti if he sees it before it runs off. Agoutis are also killed from blinds made of palm fronds stuck into the ground near fruiting trees. Such blinds are not made specifically for agoutis, but for any game animal that may come to feed on fallen fruit, including tinamous, wood-quail, acouchies, etc. The hunter simply waits inside the blind and shoots any game animals that approach. Often agoutis do not die right away when shot with an arrow; if they run off, the hunter must follow the blood trail.

The Matses cook agoutis by plucking out the large hairs on its rump, singeing and scraping of the rest of the hairs with a knife, gutting the carcass, cutting it into chunks, and boiling them without skinning. The skin is too tough to eat, but leaving the skin on preserves the tasty subcutaneous fat. There are no food taboos associated with agoutis.

Agoutis make good pets, although they run off when they grow to be adults.

MATSES NATURAL HISTORY: Agoutis have very thin front legs, a small head, large eyes, reddish ears, and a little stump for a tail. The most obvious physical characteristic of agoutis is that they are all black, except for a light-gray rump. The gray hairs extend to part of the back, where they are sparser, and even newborns have a gray rump. Agouti tracks are different from those of the paca. Older animals have thick, tough skin.

Agoutis are found in both primary and secondary forest. They are especially common in secondary forest, and they also feed in Matses swiddens.

The agouti dens in hollow logs, hollow trunks of large fallen palm trees, or in burrows, which it lines with dry leaves.

The agouti is strictly diurnal. It forages in the forest for dicot fruits. It mostly eats fruits that have fallen to the ground, but also picks fruit off branches close to the ground. Like the paca, it takes fruits to the same place to eat, near the base of the tree from which they fell, leaving a pile of remains there. It also buries fruits and nuts to eat later. It sometimes takes fruits into its den to eat or to feed its young. It does not leave the remains inside its den or near the entrance, but rather discards them some distance away. It occasionally eats mud at mineral licks.

Agoutis visit Matses swiddens to eat manioc and other crops at dawn and again from late afternoon until dusk. It eats manioc by digging up the ground that covers the tubers, starting at the stem, ruining many tubers. It sits on its haunches to eat and wiggles its ears as it eats.

Agoutis are solitary, except for mothers that travel with their young. Males and females copulate when they encounter one another while foraging during the day, but after copulating they do not stay together. When the female is ready to give birth, it makes its nest in a hollow log that it lines with many dry leaves. It gives birth to two young. It lies down with its young to suckle them, and then leaves to eat fruit. Then it come back to suckle its young again and goes out again

TABLE 32

External and Craniodental Measurements (mm) and Weights (g) of *Dasyprocta fuliginosa*
and *Myoprocta pratti* from the Yavarí-Ucayali Interfluvial Region

	D. fuliginosa[a]	*M. pratti*[b]
HBL	562 ± 6 (555–571) 5	330 ± 15 (310–343) 4
LT	21 ± 3 (18–25) 5	55 ± 3 (51–58) 4
HF	139 ± 3 (137–142) 5	89 ± 3 (83–92) 12
Ear	45 ± 5 (37–50) 5	33 ± 4 (29–39) 4
CIL	103.0 ± 4.7 (98.5–108.8) 4	66.7 ± 3.0 (61.4–71.5) 10
LD	31.6 ± 2.4 (29.9–35.7) 5	20.1 ± 1.4 (17.5–22.1) 13
MTR	21.4 ± 1.0 (20.5–22.8) 5	13.1 ± 0.4 (12.4–14.0) 13
LIF	4.7 ± 0.8 (3.7–5.7) 5	3.0 ± 0.5 (2.0–3.7) 12
BIF	3.3 ± 0.4 (2.8–3.9) 5	2.1 ± 0.2 (1.6–2.5) 12
LN	47.3 ± 3.5 (44.6–53.2) 5	23.4 ± 1.5 (19.8–25.0) 13
LIB	32.1 ± 2.0 (30.0–34.5) 5	20.7 ± 0.7 (19.2–21.6) 13
ZL	31.1 ± 1.9 (29.0–32.9) 4	21.8 ± 0.6 (20.5–22.4) 13
ZB	53.1 ± 2.3 (49.8–55.0) 4	36.6 ± 1.6 (34.3–40.6) 12
Weight	4785 ± 375 (4520–5050) 2	620 ± 0 (620) 1

[a] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 268266; FMNH 88902–88904; MUSM 11232.

[b] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 73857,73858, 73860, 73861, 74066–74070; FMNH 88908, 88909, 88911; MUSM 11234.

to feed, doing this successively during the day. When the young agoutis' teeth have grown, the mother brings fruit or pieces of manioc or plantain back to the den to feed them. When the young get larger, their mother takes them along when she goes to feed on fruit, or to swiddens to feed on manioc. When they get big, the young leave the mother permanently.

Agoutis are preyed upon by jaguars, pumas, ocelots, margays, jaguarundis, short-eared dogs, bush dogs, tayras, and grisons. They have many chiggers and small ticks around their eyes. They sometimes have a few botfly larvae.

The agouti grunts saying "tud tud tud." It barks saying "esh esh esh" when its sees people and runs off. It squeals saying "tsiod tsiod" when it is shot with an arrow.

The agouti eats mostly dicot tree fruits, including fruits of kuëte mëdiad (an unidentified tree with starchy fruits that the Matses cook before eating), bata (*Pseudolmedia* spp. or *Pere-*

bea spp. [Moraceae]), bata mapipa (*Pseudolmedia macrophylla* [Moraceae]), ṣhannëd (*Brosimum lactescens* [Moraceae]), achu inkuente (*Inga* spp. [Leguminosae-Mimosoideae]), and nëishamë ëṣhë (an unidentified tree with sweet fruits). It eats the seeds of tote (*Eschweilera* spp., *Lecythis* spp. [Lecythidaceae]) fruits. It eats the mesocarp of palm fruits in the genus *Attalea*, including ṣhuinte mapi (*A. tessmanii*), budëd (*A. butyracea*), and dapais (*A. phalerata*). It frequently eats the endosperm of pinchuk palm (*Astrocaryum murumuru*) nuts, and one can frequently find pinchuk palms sprouting where an agouti has buried their fruits. It is very fond of the mesocarp of swamp-palm (*Mauritia flexuosa*) fruits, which it piles up before eating. It also eats the mesocarp of isan palm (*Oenocarpus bataua*) fruits. It also eats the tubers of wild plants, including one called made atsa ("paca manioc," an unidentified vine whose tubers the Matses used to harvest when they were living far

from their swiddens. Agoutis frequently eat manioc that the Matses have planted, digging up the dirt with their front paws. They do not eat the whole tuber, but rather dig up many different tubers, eating bits of each (and ruining them for the Matses). They also eat ripe plantains and bananas of plants that have fallen over, and they eat ripe papayas that have fallen to the ground. In abandoned swiddens, they eat peach-palm (*Bactris gasipaes*) fruits that have fallen to the ground. The agouti also eats rotten meat, including stashed meat from jaguar kills.

REMARKS: Both specimens of *Dasyprocta fuliginosa* accompanied by habitat data from our region were shot during the daytime in secondary upland forest (abandoned swiddens). Matses observations about agouti natural history are largely consistent with published accounts of the autecology of congeneric species (reviewed and summarized by Patton and Emmons, 2015b), with the notable exception that *D. punctata* and *D. leporina* are said to live in monogamous pairs (Smythe, 1978; Dubost, 1988), whereas the Matses assert that *D. fuliginosa* is solitary.

Myoprocta pratti Pocock, 1913

Figure 44

VOUCHER MATERIAL (*N* = 20): Boca Río Yaquerana (FMNH 88909), Jenaro Herrera (MUSM 23824), Nuevo San Juan (AMNH 268267, 268268; MUSM 11234, 11235 [not seen]), Orosa (AMNH 73857–73861, 74066–74070), Quebrada Esperanza (FMNH 88910, 88911), San Fernando (FMNH 88908), Santa Cecilia (FMNH 86920). Additionally, Pavlinov (1994) reported ZMMU specimens from Jenaro Herrera that we have not seen.

UNVOUCHERED OBSERVATIONS: Río Yavarí (Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), San Pedro (Valqui, 1999, 2001).

IDENTIFICATION: Specimens of *Myoprocta* collected in the Yavarí-Ucayali interfluve exhibit all the diagnostic traits of *M. pratti* (the so-

called green acouchy), including grizzled brownish/olivaceous dorsal pelage; absence of a fringe of long, unbanded, and highly polished rump hairs; presence of a streak of white midventral hairs; a distinctive range of craniodental measurements (table 32); and widely open, teardrop-shaped sphenopalatine vacuities (Voss et al., 2001; Teta, 2019).

The taxonomy of *Myoprocta* species, commonly known as acouchies, was problematic for many years, the application of available names differing according to authors who variously emphasized geography versus pelage color to justify alternative usage. Among other relevant problems was the absence of a name-bearing type for *M. acouchy* (Erxleben, 1777), the so-called red acouchy, but this difficulty was eventually resolved by the designation of a neotype from French Guiana. Voss et al. (2001) recognized two allopatric species of *Myoprocta* distinguishable both by qualitative characters and morphometric analysis: the red acouchy from northeastern Amazonia and the green acouchy from western Amazonia. Patton and Emmons (2015a) mapped the allopatric distributions of *M. acouchy* and *M. pratti* as recognized by Voss et al. (2001), but Ramírez-Chaves et al. (2014) suggested that these species are sympatric in eastern Colombia. Teta (2019) subsequently examined some of the Colombian specimens that Ramírez-Chaves et al. (2014) referred to *M. acouchy*, reidentified them as *M. pratti*, and concluded that these species are, in fact, allopatrically distributed. To date, there has been no molecular assessment of acouchy taxonomy.

Several authors have noted geographic variation in *Myoprocta pratti* and suggested that green acouchies might comprise a species complex. Indeed, many nominal taxa are currently treated as subjective junior synonyms of *M. pratti* (e.g., by Patton and Emmons, 2015a): these include *milleri* Allen, 1913; *limanus* Thomas, 1920; *parva* Lönnberg, 1921; *archidonae* Lönnberg, 1925; *limana* Thomas, 1926; *caymanum* Thomas, 1926; and *pluralis* Thomas, 1926. Because a compre-

FIG. 44. Dorsal, ventral, and lateral cranial views of *Myoprocta pratti* (FMNH 88911). All views about ×1.2.

hensive revision of green acouchies, is beyond the scope of this report, it does not seem useful to speculate about the application of these names, although we note the relative proximity of our collections to the type locality of the nominotypical form.[29]

ETHNOBIOLOGY: The principal name for the green acouchy is tsatsin, which is not linguistically analyzable. It has one archaic synonym, choⱨoⱨ, which seems to be of onomatopoetic origin (imitating the acouchy's call). No subtypes are recognized by the Matses.

The acouchy can be classified as a minor game species, since it is quite small, infrequently killed, and not actively sought after; however, its meat is considered delicious. Acouchies are killed from hunting blinds built in the vicinity of fruiting trees. They are also, rather infrequently, killed with deadfall traps that are built principally for spiny rats (*Proechimys* spp.). They are occasionally shot when found feeding on manioc in Matses swiddens, although they are not otherwise considered to be worth a shotgun shell.

Acouchies are cooked by roasting, after singeing off the hairs and gutting (without skinning them). Acouchies are desirable pets, and hunters will take the young from burrows if they encounter any while hunting.

Young people are traditionally not allowed to eat acouchies (lest they grow thin and frail),

although nowadays this and other dietary taboos have been relaxed.

MATSES NATURAL HISTORY: The acouchy is like a small version of the agouti. The acouchy is reddish, but grizzled with white, as if its hair had begun to turn gray. Its hairs are banded. It is small and has a short, thin tail with a white tip. Its head is like a squirrel's and has whiskers on its snout. It runs very fast.

Acouchies are more common in primary than in secondary forest. They are encountered infrequently.

The acouchy dens in hollow logs, cavities at the base of hollow trees, and burrows in the ground, which it lines with dry leaves. (The Matses consider it remarkable that acouchy nests are not very deep, even nests with nursing young.)

The acouchy is strictly diurnal. It sets out at dawn and feeds all day on fallen tree fruits. When it finds ripe tree fruits, it buries them to dig up and eat later. It buries them in several holes, a bit far from the tree from which they fell. After burying fruits, it gathers more fruits into a pile and eats them. It comes back to eat more fruits in the late afternoon before retiring to its den. Where there are no ripe fruits on the ground, it digs up the fruits that it has buried. It digs into the ground searching for the palm nut or seeds of fruits it has buried, even if the ground is muddy. It wags its little tail as it comes to eat, and it wipes its snout with its forefeet after eating to clean off any residue. It drinks muddy water at mineral licks.

The acouchy is solitary. It raises its young in hollow logs or holes in the ground. It brings fruit to its den to feed its young.

Acouchies are preyed upon by ocelots, margays, jaguarundis, short-eared dogs, bush dogs, tayras, hawks, and eagles.

The acouchy yells out "chochochosh" as it flees when it sees people.

The acouchy principally eats dicot tree fruits of many types, especially those of bata (*Pseudolmedia* spp. or *Perebea* spp. [Moraceae]) and bata mapipa (*Pseudolmedia macrophylla* [Moraceae]). It also eats the seeds of dicot tree fruits whose

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[29] The type locality of *Myoprocta pratti* is not immediately obvious from the primary literature, although there is no substantive disagreement on this point among the secondary sources cited above. Pocock's (1913: 110–111) original description was based on two specimens: the type (BMNH 13.7.17.1), said to have been presented to the Zoological Society by one Mr. Chavez, who brought it from the "Amazons," and a paratype (BMNH 17.3.21.1) collected by a Mr. Pratt in Peru. Thus, Pocock's text suggests that the type locality should be the "Amazons" (i.e., Amazonia), but Thomas (1920, 279, fn.) explained that Pratt collected his agoutis [sic] at the Pongo de Rentema on the Marañón, and a note in Thomas's distinctive handwriting on the skin tag of BMNH 17.3.21.1 states that both specimens (Chavez's and Pratt's) were from the same expedition. The Pongo de Rentema (5°29′S, 78°31′W; DMA, 1989) is a narrow cataract just below the confluence of the Marañón with the Río Utcubamba on the border between the departments of Cajamarca and Amazonas, about 540 km west of our region.

pulp has rotted away, including seeds of tonnad (a general term for trees in the family Myristicaceae). It also eats the endosperm of pinchuk palms (*Astrocaryum murumuru*). It eats manioc in Matses swiddens.

REMARKS: Three of the four specimens of *Myoprocta pratti* accompanied by capture data from our region were trapped on the ground in secondary upland forest (abandoned swiddens), but one was trapped on the ground in primary upland forest. Matses observations about green acouchies are entirely consistent with, and substantially complement, previously published accounts of *Myoprocta* behavior (e.g., Dubost, 1988; Emmons, 1997).

Dinomyidae

Dinomys branickii Peters, 1873

Figure 45

VOUCHER MATERIAL (*N* = 1): Nuevo San Juan (MUSM 11231). In addition to our single specimen, the occurrence of *Dinomys branickii* in the Yavarí-Ucayali interfluve is documented by photographs of one adult and a juvenile that were killed by a Matses man at Estirón in 2013. The dead individuals were examined by D.W.F., but they were not preserved because he had no collecting permits for them. Unfortunately, the photographs are not suitable for publication.

UNVOUCHERED OBSERVATIONS: None.

IDENTIFICATION: Our single specimen of *Dinomys branickii*—commonly known as the pacarana—consists of the skull of an adult individual (with fused basicranial sutures). Although incomplete, this specimen exhibits all the diagnostic craniodental traits of this morphologically unique taxon (Patton, 2015c). Selected measurements of MUSM 11231 are: condyloincisive length, 144.9 mm; length of diastema (alveolar), 35.2 mm; maxillary toothrow (alveolar), 33.3 mm; length of nasals, 54.8 mm; least interorbital breadth, 54.4 mm; zygomatic length, 57.4 mm; and zygomatic breadth, 99.0 mm. The photographs of dead individuals from Estirón are equally compelling

because they clearly show the diagnostic external traits of pacaranas as described by authors (Emmons, 1997; Patton, 2015c).

Apparently, our specimen and photographs constitute the only definite records of *Dinomys branickii* from Loreto department.[30]

ETHNOBIOLOGY: The Matses name for the pacarana is tambisbiekkid ("one that is similar to a paca"). A dialectal variant name is tambis inkuente chokid ("paca that has a tail"). Despite these names, it is not considered a type of paca. No subtypes are recognized by the Matses.

Pacaranas are encountered infrequently, so not all Matses have seen them. They do not seem to occur in all parts of Matses territory, such as along the lower Río Gálvez, whereas they are more common along the upper Gálvez and the upper Quebrada Chobayacu. The Matses do not eat pacaranas, which are sometimes seen while hunting or are flushed from their burrow by hunting dogs during the day. Sometimes a hunter mistakes a pacarana for a paca when dogs chase one into a hole. When the hunter catches up, he introduces a palm frond into the burrow; if the quarry bites it (something that pacas never do), he knows that it is a pacarana.

Pacaranas can be pests in Matses swiddens. They don't just eat some of the tubers (like pacas do), but they also cut away the stem, killing the whole plant. They return every night to the swidden until they are killed. To be rid of pacaranas that have become pests, Matses search the area around the swidden with dogs,

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[30] The specimen that Patton (2015c) listed from Iquitos (AMNH 98576) was part of a large collection of Amazonian vertebrates that Harvey Bassler donated to the AMNH in 1934, but the locality datum is problematic. The fauna of Iquitos and its evirons on the left (north) bank of the Amazon, has been intensively surveyed for many years (most recently by Hice and Velazco, 2012), and it is implausible that a mammal as large as *Dinomys branickii* (ca. 10–15 kg) should not be represented by additional specimens or observations if it really occurred there. Harvey Bassler—a petroleum geologist and amateur collector of natural history specimens throughout much of western Amazonia (Willard, 1966; Edson, 1982; Myers, 2000)—is known to have maintained a small zoo at Iquitos, and his manuscript catalog of mammals (in the Department of Mammalogy archives) records the locality of AMNH 98576 as "Iquitos (prep.)." We infer that this specimen was captured elsewhere but died in his menagerie.

FIG. 45. Ventral cranial view (about ×0.75) of a salvaged skull of *Dinomys branickii* (MUSM 11231).

hunt them down, and kill them. However, if pacaranas are encountered far from swiddens, the Matses do not kill them.

Matses natural history: The pacarana's head and body are like a paca's, but it has a tail. It has longitudinal stripes on its body and has a large head.

The pacarana dens in a shallow hole in a stream headwater gully or in standing hollow trees that have a hole at the base.

It is nocturnal. During the night it forages for dicot tree fruits in the forest and comes to eat manioc in swiddens.

It is solitary.

It enters any hole for refuge when dogs pursue it. Unlike the paca, it does not plunge into streams when pursued.

The pacarana eats principally dicot tree fruits. It also eats the stems of mani pada plants (*Heliconia* spp. [Heliconiaceae]). In Matses swiddens it feeds mostly on manioc tubers, but also on ripe or unripe plantain fruits and sugar cane.

Remarks: The single collected specimen and both photographed individuals of *Dinomys branickii* from our region were killed in Matses swiddens. The skull from Nuevo San

Juan was discarded and left outdoors near the village, where it was defleshed by scavengers and insects; the mandibles and missing teeth could not be found. Matses natural history observations about this species are sparse, but their assertion that it is solitary appears to contradict published suggestions that pacaranas live in pairs or small groups (White and Alberico, 1992; Saavedra-Rodríguez et al., 2012). By contrast, Matses dietary observations are consistent with published observations that this species eats tubers, succulent stems, and fruit, but not seeds (Neto et al., 2017; González and Osbahr, 2013). Its exceptionally broad incisor teeth; convergent toothrows; and hypsodont, ever-growing cheekteeth suggest that *Dinomys* routinely consumes soft but abrasive items, presumably tubers and rhizomes, which we conjecture to be dietary staples of this unusual rodent.

Erethizontidae

The taxonomy of Neotropical porcupines has undergone substantial changes in recent years, the result of species-level revisionary work and subsequent phylogenetic analyses (Voss, 2011, 2015; Menezes et al., 2021). Two species are known from our region, and no others can plausibly be expected to occur there.[31] All Neotropical porcupines are arboreal, nocturnal, have weak eyeshine, and do not normally vocalize. Therefore, they are seldom observed, and only one of our two local species is vouched by collected specimens.

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[31] *Coendou bicolor* has been reported (or listed as "expected") in our region by several authors (e.g., Ríos et al., 1974; Valqui, 1999, 2001; Salovaara et al., 2003; Amanzo, 2006; Escobedo-Torres, 2015) based on misapplications of this name in field guides and other references (e.g., Emmons, 1997; Eisenberg and Redford, 1999). However, *C. bicolor* is apparently restricted to montane or premontane habitats in northern Peru; only in southern Peru is this species known to occur in the Amazonian lowlands (Voss, 2011, 2015). We assume that all unvouchered records of *C. bicolor* from the Yavarí-Ucayali interfluve are based on misidentifications of *C. longicaudatus* as recognized in this report.

Coendou ichillus Voss and da Silva, 2001

Figure 46

VOUCHER MATERIAL: None.

UNVOUCHERED OBSERVATIONS: El Chino (Carter, 2023).

IDENTIFICATION: Originally described from eastern Ecuadorean material, *Coendou ichillus* has subsequently been reported from scattered sites throughout western Amazonia (e.g., Gregory et al., 2015; Ramírez-Chaves et al., 2016, 2020; Menezes et al., 2020). This taxon is easily distinguished in the field from its broadly sympatric congener *C. longicaudatus* (formerly *C. prehensilis*; see below) by its much smaller adult size and by several conspicuous external traits (table 33). Should skeletal material eventually be collected in our region, cranial comparisons are equally diagnostic. Among other qualitative differences, *C. ichillus* has a dorsally flattened skull (Voss and da Silva, 2001: figs. 10, 11), whereas *C. longicaudatus* has a conspicuously convex dorsal cranial profile due to its hugely inflated frontal sinuses (fig. 47). Additionally, cranial measurements of *C. ichillus* do not overlap those of *C. longicaudatus*: condyloincisive length, for example, is 59–64 mm in the former species versus 78–97 mm in the latter, and crown length of the maxillary toothrow is 14–15 mm versus 19–22 mm (Voss and da Silva, 2001; Voss, 2010). Weight data is unavailable for this species.

ETHNOBIOLOGY: Although a few Matses hunters have reported seeing a small porcupine that might correspond to this species, they do not recognize it as a distinct species.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: As reported by Carter (2023; personal commun.), two solitary individuals of *Coendou ichillus* were located at night using thermal imaging technology in the subcanopy of seasonally flooded primary forest near Tahuayo Lodge, an ecotourist facility about 2 km WSW of El Chino.

TABLE 33

Diagnostic External Characters of *Coendou ichillus* and *C. longicaudatus*

	C. ichillus	*C. longicaudatus*
Size[a]	HBL = ca. 260–295 mm, HF = 55–59 mm	HBL = 403–530 mm, HF = 82–105 mm
Defensive quills[b]	bicolored only (except on head)	tricolored & bicolored
Bristle quills[b]	very long, tricolored	absent
Caudal bristles[b]	black	pale-tipped brown
Muzzle	not swollen	swollen and bulbous

[a] Measurements of *Coendou ichillus* from Voss and da Silva (2001) Ramírez-Chaves et al. (2016), and Menezes et al. (2020); measurements of *C. longicaudatus* from Voss (2010). Because the sample size for *C. ichillus* is small (*N* = 5), it is probable that the range of metrical variation in this species is underestimated.

[b] For definitions of erethizontid pelage structures, see Voss (2015: 787–788).

Coendou longicaudatus Daudin, 1802

Figure 47

Voucher material (*N* = 6): Nuevo San Juan (AMNH 268263, 273130; MUSM 11224, 15325), Santa Cecilia (FMNH 86916, 86917). Additionally, Pavlinov (1994) recorded a single ZMMU specimen (as "*Coendou ?bicolor*") from Jenaro Herrera that we have not seen.

Unvouchered observations: El Chino (Carter, 2023), Jenaro Herrera (Ríos et al., 1974; Tovar, 2011), San Pedro (Valqui, 1999, 2001).[32]

Identification: *Coendou longicaudatus* has traditionally been synonymized with *Coendou prehensilis* (Linnaeus, 1758), but recently analyzed morphological and molecular data suggest that it is a distinct species (Menezes et al., 2021). Our voucher material agrees in all respects with Husson's (1978: 478–484) detailed description of nearly topotypical material (from Surinam), and measurements of our series (table 34) fall within the previously documented range of morphometric variation in this very widespread species (Voss, 2011: table 7). Cytochrome *b* sequence data from two of our vouchers (AMNH 273130, MUSM 15324) were analyzed by Voss et al. (2013) and Menezes et al. (2021), both of whom documented the surprising genetic

homogeneity of *C. longicaudatus* across its enormous geographic range (see below).

According to Menezes et al. (2021), the *Coendou prehensilis* complex includes three valid species: (1) *Coendou prehensilis* (sensu stricto), which occurs in the easternmost Brazilian states of Alagoas, Paraíba, and Pernambuco; (2) *C. longicaudatus*, which occurs from Colombia, Venezuela, and the Guianas throughout most of Amazonia and the Cerrado to Paraguay and northwestern Argentina; and (3) *C. baturitensis* Feijó and Langguth, 2013, which occurs in the Brazilian states of Ceará, Maranhão, and Pará (south of the Amazon and east of the Rio Xingu). Although we have not seen material of *C. prehensilis* in its currently restricted sense, we recently examined two specimens of *C. baturitensis* (from Cameta, on the left bank of the Rio Tocantins: MCZ 30556, 30557) that precisely match the diagnostic traits of that species as listed by Menezes et al. (2021: table 2). Taken together with the authors' sequencing results, the case for recognizing three valid species in the *C. prehensilis* complex now seems compelling (contra Voss, 2015). However, some of Menezes et al.'s diagnostic comparisons fail to acknowledge individual and/or geographic variation in *C. longicaudatus*. For example, the lacrimal was said to be indistinguishably fused to surrounding cranial bones even in neonatal specimens, but open-sutured lacrimals are present in some juveniles (e.g., AMNH 268263), and some lacrimal sutures

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[32] Most unvouchered reports of porcupines from our region have misidentified this species as *Coendou bicolor* (see above).

FIG. 46. *Coendou ichillus* photographed at night by Paul Carter in the subcanopy of seasonally flooded primary forest near Tahuayo Lodge (about 2.4 km WSW of El Chino) on 23 June 2023. Four diagnostic traits (unswollen muzzle, bicolored defensive quills, tricolored bristle quills, and black caudal bristles) are visible in this photo.

occasionally persist even in fully adult individuals (e.g., MUSM 15324). We also note that, although *C. prehensilis* (sensu stricto) has substantially smaller craniodental measurements than Brazilian populations of *C. longicaudatus* (see Menezes et al., 2021: table 2), *C. prehensilis* is about the same size as specimens of *C. longi-*

caudatus from northern Colombia (Voss, 2011: table 7), and we doubt that these species could be distinguished morphometrically if such geographic variation were taken into account.

ETHNOBIOLOGY: The Matses name for the long-tailed porcupine is <u>isa</u>, which is cognate with the name for porcupine in most other

Panoan languages. The Matses do not recognize any subtypes of this species. A few Matses have reported seeing another type of porcupine that is said to be smaller, but it is not certain whether they are referring to a different species or to juvenile individuals of *C. longicaudatus.*

Porcupines are not eaten by the Matses, who have no other economic interest in them. Porcupines occasionally enter Matses houses, and when this happens, the Matses believe it to be an omen that someone in the household will soon die. Dogs are sometimes injured by quills when they try to bite a porcupine.

Matses natural history: The porcupine has teeth like a paca's. It has whiskers on its snout, and its eyes are close to its nose. It has long, sharp quills on its body, and shorter spines on its head and tail, although the top of the end of the tail (the prehensile surface) is free of spines. The quills are banded and detach easily when the porcupine is hit with a stick. Porcupines have a strong, distinctive smell that can be detected from a long distance away.

The porcupine is mostly arboreal, but also comes down to the ground. Porcupines are not seen very often, and not all Matses have seen them.

It dens in holes in trees. It also sleeps on tree branches, usually where there is a vine tangle that provides some shelter.

The porcupine is nocturnal. It can climb trees and vines quickly. During the night, it feeds on the bark of tree branches or on the bark of the trunks of small trees (i.e., they do not feed on the trunks of large trees, presumably because they cannot cling to them). It comes down to the ground to feed on rotten tree stumps, to eat the rinds of fallen palm nuts, and occasionally to eat mud at mineral licks.

It chews noisily on bark.

The porcupine eats tree bark, including the bark of dead trees. It also eats the rind of palm nuts that have fallen to the ground long ago (especially those of the genus *Attalea*, including budëd [*A. butyracea*])

Remarks: All four specimens of *Coendou longicaudatus* accompanied by capture data from our region were taken in primary floodplain (seasonally inundated) forest. Two were shot at night as they ate bark in the subcanopy (about 20–25 m above the ground), whereas a male-female pair were shot in the daytime as they rested "very high up in a tree hole" (possibly the central cavity of a hollow tree; D.W.F. field notes, 1 October 1999). Matses observations are consistent with what little is known about the behavior of this species (reviewed by Voss, 2015), notably including its visits to mineral licks (Griffiths et al., 2020).

Echimyidae

The Yavarí-Ucayali interfluve is rich in echimyid rodents, including one species each of *Dactylomys*, *Isothrix*, *Makalata*, *Mesomys*, and *Toromys*, and six species of *Proechimys*. Echimyid classification has undergone many changes in recent years as the result of progress in both morphology-based and molecular research. Although Emmons et al. (2015a) classified the species treated in this report as members of three subfamilies (Dactylomyinae, Echimyinae, and Eumysopinae), all Amazonian echimyids are now placed in the subfamily Echimyinae (Fabre et al., 2017; Courcelle et al., 2019). As currently recognized, this subfamily includes a diverse radiation of arboreal taxa (tribe Echimyini) and a clade of predominantly terrestrial taxa (tribe Myocastorini). Of the six genera known to occur in our region, five (*Dactylomys*, *Isothrix*, *Makalata*, *Mesomys*, and *Toromys*) belong to the tribe Echimyini, whereas *Proechimys* belongs to the tribe Myocastorini. In the absence of a published key to echimyine genera,[33] we summarize selected diagnostic comparisons of the taxa in our region (table 35), and we preface the taxonomic accounts that follow with brief descriptions of salient morphological traits.

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[33] To identify echimyine genera using the keys in Patton et al. (2015), it is necessary to start with the key to echimyid subfamilies.
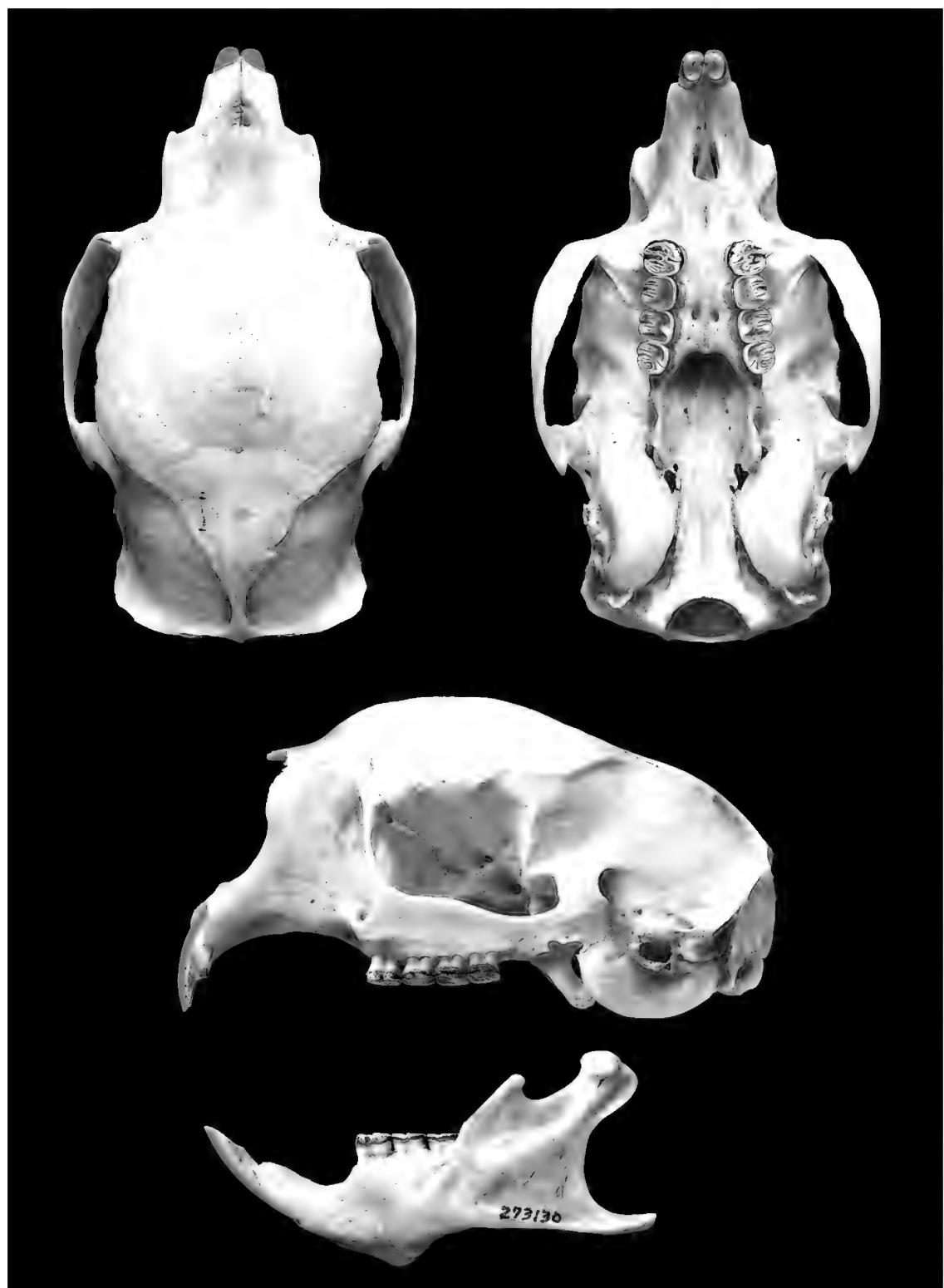
TABLE 34

**External and Craniodental Measurements (mm) and Weights (g) of *Coendou longicaudatus*
from the Yavarí-Ucayali Interfluve**

	AMNH 273130♂	FMNH 86916♂	FMNH 86917♀	MUSM 11224♀	MUSM 15324♀	Sample
HBL	495	480	460	500	458	479 ± 19
LT	465	470	500	455	456	469 ± 18
HF	96	90	"76"	95	94	94 ± 3
Ear	31	29	25	30	28	29 ± 2
CIL	96.7	95.2	89.6	90.9	90.8	92.6 ± 3.1
LD	26.6	28.9	23.9	24.8	22.7	25.4 ± 2.5
MTR	21.9	20.1	20.6[a]	21.0	21.0	20.9 ± 0.6
LIF	6.2	5.4	5.9	4.7	5.4	5.5 ± 0.6
BIF	4.4	4.5	4.5	4.1	4.0	4.3 ± 0.2
LN[b]	—	—	32.4	—	—	—
LIB[c]	37.0	35.6	34.3	40.0	41.8	37.7 ± 3.1
ZL	37.8	36.7	35.2	35.9	35.5	36.2 ± 1.0
ZB	55.0	56.2	53.8	55.2	56.2	55.3 ± 1.0
Weight	4100	—	—	3800	3780	3893 ± 179

[a] Estimated value.
[b] The nasal bones are often indistinguishably fused to the frontals in fully adult porcupines, so their length can seldom be measured.
[c] Measured across the swollen frontal sinuses.

Echimyids appear to exhibit indeterminate growth (Patton and Rogers, 1983; Pessoa and Dos Reis, 1991), and many collected specimens are immature, so age determination is important for meaningful taxonomic comparisons. As noted above, there is no premolar replacement in echimyids, so the adult maxillary dentition consists of dP4–M3, of which M3 is the last tooth to erupt. We regard adult individuals as those in which at least some dentine is exposed by wear on all the transverse crests of M3, corresponding to age classes 8–10 of Patton and Rogers (1983).

The Matses refer to arboreal and terrestrial echimyids by different names, which are the basis for ethnobiological observations and interviews summarized under separate headings below.

Echimyini (arboreal echimyids)

Echimyine systematics has long been problematic, but the sustained efforts of several researchers have transformed our taxonomic understanding of this interesting radiation of arboreal caviomorphs (Emmons et al., 2015a; Fabre et al., 2017; Emmons and Fabre, 2018; Courcelle et al., 2019). Five species of echimyines (one each of *Dactylomys*, *Isothrix*, *Makalata*, *Mesomys*, and *Toromys*) are known to be present in the Yavarí-Ucayali interfluve.

ETHNOBIOLOGY: The general term for tree rats is <u>abuk maka</u> ("up rat," <u>maka</u> being an archaic general term for small rodents), which is included in the general category for rats and mice, <u>tambisëmpi</u>. Two subtypes of <u>abuk maka</u>

FIG. 47. Dorsal, ventral, and lateral cranial views of *Coendou longicaudatus* (AMNH 273130). All views about ×0.95.

TABLE 35

Selected Diagnostic Traits of Echimyid Genera

	Echimyini					Myocastorini
	Dactylomys	*Isothrix*	*Makalata*	*Mesomys*	*Toromys*	*Proechimys*
Dorsal pelage	soft	soft	spiny	spiny	spiny[a]	spiny
Manual digits[b]	II<<III=IV>>V	II<III=IV>V	II<III=IV>V	II<III=IV>V	II<III=IV>V	II<III>IV>V
Manual ungues	blunt nails	sharp claws	sharp claws	sharp claws	sharp claws	sharp claws
Tail[c]	naked & scaly, no terminal tuft	densely haired, w/ terminal tuft	naked & scaly, no terminal tuft	sparsely haired, w/ terminal tuft	sparsely haired, no terminal tuft	naked & scaly, no terminal tuft
Tail length (TL)[d]	>>HBL	>HBL	<HBL	variable	<HBL	<<HBL
Maxillary toothrows	convergent	parallel	parallel	parallel	parallel	parallel
Labial flexi[e]	patent	patent	patent	closed	patent	closed

[a] Spines of *Toromys* spp. have soft tips, so they do not feel sharp.
[b] Abbreviations: <<, much shorter than; <, shorter than; =, equal in length; >, longer than; >>, much longer than.
[c] Macroscopic appearance (even seemingly naked tails have short caudal hairs that are visible under magnification).
[d] Relative to head-and-body length (HBL)
[e] Of adult upper cheekteeth. Closed labial flexi form elongated, transversely or obliquely oriented enamel islands on the occlusal surface.

are recognized and named by the Matses: <u>abuk maka dëtan</u> ("striped-nosed tree rat," which designates *Isothrix bistriata*) and <u>abuk maka kapinchuk</u> ("spiny-backed tree rat," which designates *Makalata* sp. and *Mesomys hispidus*).[34] The Matses are not sufficiently familiar with tree rats to recognize additional species.

Tree rats are not eaten by the Matses and are infrequently encountered. They are not pests or kept as pets, so they are not killed or captured. *Isothrix bistriata* is sometimes seen poking its head out of tree holes, and tree rats are also sometimes encountered while felling trees for swiddens.

Matses natural history: Tree rats resemble spiny rats (*Proechimys* spp.), but they have furry tails and light-colored (but not white) undersides. Some have spiny, flat bristles on their backs. Some have a stripe on the forehead.

Tree rats are arboreal, but occasionally they come down to the ground to forage. Tree rats are found in primary forest. They are seldom observed.

They live up in tree holes, which they line with dead leaves.

Tree rats are nocturnal. During the day they may stick their heads out of their holes when a person is walking past. At night they forage for fruits that they pick off the branches and bring back to eat sitting on a branch near their dens. Occasionally they come down to the ground to eat fruits. When they descend to the ground, they do so by climbing down a liana. They return to their dens at dawn.

They are solitary.

They are preyed on by margays, kinkajous, and arboreal pitvipers.

Tree rats eat dicot tree fruits, including those of <u>bata</u> (*Pseudolmedia* spp, or *Perebea* spp. [Moraceae]), <u>bata mapipa</u> (*Pseudolmedia macrophyllum* [Moraceae]), and <u>shëshun</u> (*Spondias mombin* [Anacardiaceae]). They also eat the

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[34] To date, *Dactylomys dactylinus* and *Toromys rhipidurus* have not been collected in Matses territory, although they are known to occur elsewhere in the Yavarí-Ucayali interfluve (see below).

fruits of <u>tonnad</u> (a general term for trees in the family Myristicaceae).

Dactylomys dactylinus (Desmarest, 1817)

Figure 48

VOUCHER MATERIAL ($N = 16$): Orosa (AMNH 73771–73786). In addition, Pavlinov (1994) reported a single ZMMU specimen from Jenaro Herrera that we have not seen.

UNVOUCHERED OBSERVATIONS: Río Yavarí (Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), San Pedro (Valqui, 1999, 2001).

IDENTIFICATION: Dactylomys dactylinus is a large rat (600–700 g; Emmons, 1997) with soft fur and a long, macroscopically naked, and visibly scaly tail. The dorsal body pelage is blackish coarsely streaked with pale yellow, but the head is uniformly pale brown, and the backs of the thighs are bright rufous; the ventral coloration is self-white from chin to anus. Unlike any other arboreal rodent in our region, the digits of the manus are provided with blunt nails rather than sharp claws, and the two middle digits (III and IV) are equal in length and much longer than the outer digits (II and V). The cheekteeth are prismatic, and the upper toothrows are strongly convergent anteriorly. In these and other details—including external and craniodental measurements (table 36)—our specimens closely match the morphological descriptions of D. dactylinus provided by Patton et al. (2000) and Emmons et al. (2015b), who discussed unresolved taxonomic issues concerning the unknown type locality. We are aware of ongoing taxonomic research on bamboo rats (for which tissues have been taken from AMNH specimens for DNA sequencing), so we have not undertaken any further effort to identify our material.

ETHNOBIOLOGY: This species is not known to the Matses, who have no special name for it.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: Dactylomys dactylinus is typically, although not exclusively, found in the floodplains of white-water rivers, where the presence of this nocturnal, herbivorous species is conspicuous by its loud nocturnal barking from bamboo and canebrakes (Emmons, 1981). The absence of Dactylomys from the vicinity of Nuevo San Juan can be inferred from the fact that the Matses there are unfamiliar with it, but multiple unvouchered observations suggest that bamboo rats may occur widely in riparian habitats elsewhere in our region. No habitat data accompany the Olalla's series from Orosa, but their specimens were almost certainly collected in várzea, which extends inland for several kilometers from the right bank of the Amazon at this locality (Wiley, 2010: 40).

Isothrix bistriata Wagner, 1845

Figures 49, 50

VOUCHER MATERIAL ($N = 16$): Nuevo San Juan (AMNH 268271, 268272, 272808, 273056; MUSM 11243, 11247, 11248, 13305, 15325, 15326), Orosa (AMNH 73788, 73789, 74071–74073), Zarate on Río Manatí (FMNH 112566).

UNVOUCHERED OBSERVATIONS: Río Yavarí (Salovaara et al., 2003), San Pedro (Valqui, 1999, 2001).

IDENTIFICATION: Isothrix bistriata is a large, soft-furred (not spiny) grizzled-brownish rat with a pale (whitish) midfrontal blaze separating two black supraorbital stripes that extend posteriorly onto the nape; the ventral fur is gray-based yellowish or buffy. Unlike Dactylomys (the only other soft-furred arboreal echimyid in our region), the manual digits have strong, sharp claws, and the tail is densely covered with long, soft, outwardly curving hairs that are reddish at the base of the tail but blackish distally. In these and other morphological details (including external and craniodental measurements; table 37), our material closely matches the description provided by Emmons and Patton (2015a), who treated sev-
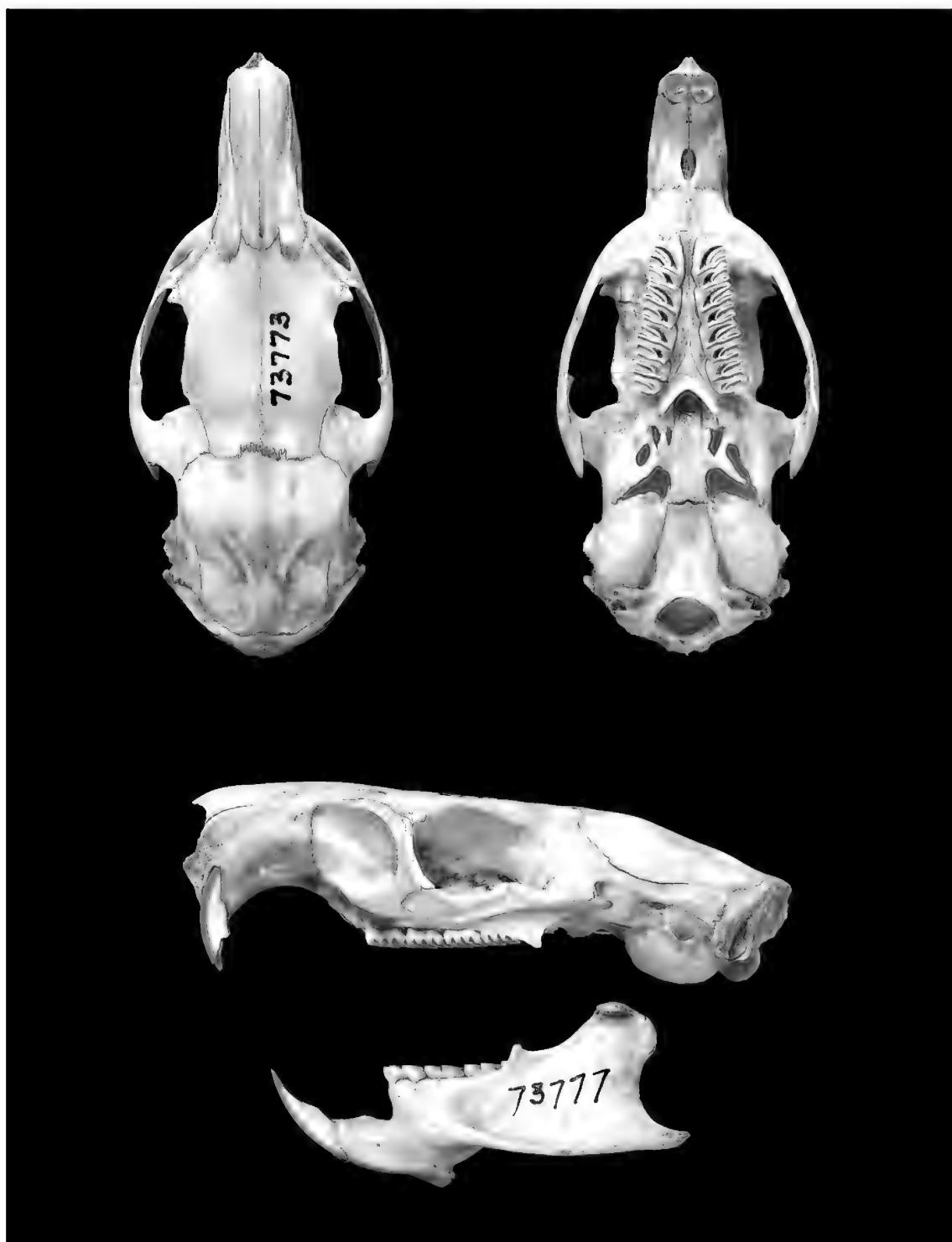
FIG. 48. Dorsal, ventral, and lateral cranial views of *Dactylomys dactylinus* (skull: AMNH 73773; mandible: AMNH 73777). All views about ×1.2.

TABLE 36

Measurements (mm) of *Dactylomys dactylinus* from the Yavarí-Ucayali Interfluve[a]

HF	61 ± 2 (57–65) 14
CIL	69.3 ± 2.8 (63.2–72.6) 14
LD	16.8 ± 0.8 (15.2–18.1) 15
MTR	19.2 ± 0.6 (17.8–20.3) 15
LIF	4.1 ± 0.7 (3.0–5.3) 14
BIF	2.0 ± 0.3 (1.7–2.6) 15
LN	24.4 ± 1.1 (22.2–26.0) 15
LIB	19.2 ± 1.8 (16.9–23.0) 14
ZL	27.2 ± 1.3 (24.2–29.0) 15
ZB	35.9 ± 1.3 (33.4–38.6) 14

[a] Tabulated statistics are the mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 73771–73782, 73784–73786.

eral nominal taxa (*villosa* Deville, 1852; *molliae* Thomas, 1924; and *boliviensis* Petter and Cuenca-Aguirre, 1982) as subjective junior synonyms and recognized *I. negrensis* Thomas, 1920—the "downstream clade" of *I. bistriata* sensu Patton et al. (2000: 179–186)—as a distinct species. The external characteristics of this species are sufficient for confident identification of photographs taken by ecotourists at several localities in our region (e.g., fig. 50).

ETHNOBIOLOGY: The Matses have no special name for this species.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: Of 10 specimens of *Isothrix bistriata* accompanied by habitat information from our region, seven (including an adult female with a juvenile offspring) were extracted from tree holes during the daytime by various means; recorded heights of the tree holes from which specimens were collected ranged from 15 to 40 m above the ground. Three additional specimens were shot at night as they perched on branches or clung to vertical trunks in the subcanopy. Although nine of our specimens were collected in seasonally flooded forest—said to be the usual habitat of the species (Pat-

ton et al., 2000: 185)—one was taken in primary terra firme forest. According to Valqui (2001), this species occurs along rivers near San Pedro, where it nests in hollow trees.

Makalata "species 5"

Figure 51

VOUCHER MATERIAL (TOTAL = 4): Nuevo San Juan (AMNH 268270; MUSM 11241, 11242, 15327).

UNVOUCHERED OBSERVATIONS: None.

IDENTIFICATION: Specimens of *Makalata* from the Yavarí-Ucayali interfluve have dorsal pelage composed of soft fur mixed with strong, flat, sharp spines. The dorsal coloration (best preserved in MUSM 11242) is grizzled tawny over the middle back and hips but grayish brown on the crown of the head, nape, forelegs, shoulders, and flanks; by contrast, the nose and eye rings are reddish, as is the fur at the base of the tail. The ventral pelage is grizzled grayish brown and does not contrast sharply in color with the dorsal pelage. The visibly scaly tail is shorter than the combined length of the head and body and lacks a terminal tuft of long hairs. Digits II–V of the forefoot are provided with strong, sharp claws, and digit III is about the same length as digit IV. The maxillary toothrows are parallel, and the labial flexi are patent. In these and other morphological traits (including external and craniodental measurements; table 37), our specimens resemble the descriptions of *M. macrura* (Wagner, 1842) in Patton et al. (2000) and Emmons and Patton (2015b), but the application of Wagner's name to our material is problematic.

Patton et al. (2000) and Emmons and Patton (2015b) recognized only two valid species of *Makalata*: *M. macrura* in western Amazonia and *M. didelphoides* (Desmarest, 1817) in eastern Amazonia.[35] This dichotomy was based on

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[35] A third name, *Makalata obscura* (Wagner, 1840) was listed by Emmons and Patton (2015b) as though it applied to a valid species, but by their own admission it is a nomen dubium.

FIG. 49. Dorsal, ventral, and lateral cranial views of *Isothrix bistriata* (MUSM 11247). All views about ×1.6.

FIG. 50 *Isothrix bistriata* photographed by Wayne W. Godbehere on 10 May 2015 on the left bank of the Río Tahuayo just upstream from El Chino.

the discovery of strongly supported mtDNA clades with geographic distributions corresponding to those attributed to the species, and by plausible inferences about the application of names based on known or presumed type localities. More recently, however, analyses of karyotypes and molecular data (Miranda et al., 2021) suggest the existence of numerous morphologically cryptic species of *Makalata*. Although Miranda et al.'s phylogenetic analyses of cytochrome *b* sequences recovered strongly supported eastern and western Amazonian clades—consistent with Patton et al.'s (2000) results—one sequence from a specimen collected near the type locality of *M. macrura* (on the right bank of the lower Rio Madeira) was recovered as part of a haplogroup within the eastern Amazonian clade, whereas a sequence from the Yavarí-Ucayali interfluve

(obtained from MUSM 15327)[36] together with Patton et al.'s (2000) sequences from the Rio Juruá were recovered as a haplogroup ("species 5") belonging to the western clade. Based on sequences that we downloaded from GenBank, the uncorrected average difference between "species 5" (represented by L23356, L23357, MW965251, and MW965235) and *M. macrura* (as restricted by Miranda et al., 2021: represented by MW965236, MW965237, MW965242, and MW965243) is about 14% at the cytochrome *b* locus.

Based on these analytic results, the name *Makalata macrura* cannot be applied to our material.

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[36] Confusingly, Miranda et al. (2021: table 2) incorrectly associated MUSM 15327 and its cytochrome *b* sequence (MW965251) with a Brazilian locality, and they also incorrectly attributed the sequence to Patton et al. (2000). As noted above, MUSM 15327 was collected at Nuevo San Juan, and its sequence was not among those analyzed by Patton et al. (2000: table 53).

TABLE 37

Measurements (mm) and Weights (g) of Four Arboreal Echimyids from the Yavarí-Ucayali Interfluve

	Isothrix bistriata[a]	*Makalata* sp. 5[b]	*Mesomys hispidus*[c]	*Toromys rhipidurus*[d]
HBL	235 ± 21 (199–255) 7	219, 252	190 ± 6 (184–195) 3	243 ± 11 (227–251) 4
LT	245 ± 18 (223–275) 7	191, 204	179 ± 14 (170–195) 3	197 ± 17 (180–219) 4
HF	46 ± 2 (44–50) 8	39, 42	33 ± 2 (31–35) 5	42 ± 3 (37–44) 4
Ear	17 ± 1 (15–19) 8	15, 15	14 ± 2 (11–16) 5	17 ± 2 (15–19) 4
CIL	50.3 ± 1.8 (48.1–54.0) 13	46.1, 49.2	39.5 ± 2.4 (36.8–42.2) 4	49.9 ± 2.3 (46.1–51.7) 7
LD	12.1 ± 0.6 (11.0–13.0) 13	11.1, 12.3	9.7 ± 0.7 (8.8–10.6) 5	12.4 ± 0.9 (11.0–13.4) 7
MTR	10.9 ± 0.3 (10.4–11.4) 13	11.6, 11.3	7.6 ± 0.2 (7.1–7.8) 7	12.3 ± 0.4 (11.9–12.9) 7
LIF	5.3 ± 0.8 (4.3–7.0) 12	3.6, 3.3	3.8 ± 0.3 (3.4–4.2) 5	4.7 ± 0.7 (3.6–5.4) 6
BIF	2.2 ± 0.4 (1.5–2.7) 13	1.8, 1.8	1.7 ± 0.2 (1.4–1.8) 5	2.2 ± 0.4 (1.6–2.5) 6
LN	15.7 ± 0.9 (14.1–16.9) 11	15.5, 17.0	12.9 ± 1.1 (11.2–14.2) 5	17.1 ± 1.2 (14.9–18.7) 7
LIB	13.6 ± 0.6 (12.6–14.4) 12	11.4, 12.2	11.4 ± 0.7 (10.6–12.3) 5	14.4 ± 0.8 (13.3–15.3) 7
ZL	19.6 ± 0.8 (18.4–21.3) 13	18.8, 20.2	16.0 ± 1.1 (14.6–17.4) 6	20.7 ± 0.9 (19.4 –21.6) 7
ZB	28.8 ± 1.2 (26.7–31.5) 13	24.7, 26.5	22.6 ± 1.3 (20.6–24.3) 5	27.4 ± 1.0 (26.0–29.1) 7
Weight	399 ± 75 (340–561) 8	269, 321	216 ± 24 (195–246) 4	455 ± 110 (330–535) 3

[a] Tabulated statistics are the mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 73788, 73789, 74071–74073, 268271, 268272, 272808; MUSM 11243, 11247, 11248, 15325, 15326.

[b] Measurements of AMNH 268270 and MUSM 11242.

[c] Tabulated statistics are the mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 268252, 268269, 273080; FMNH 87242; MUSM 13306, 15328, 22346.

[d] Tabulated statistics are the mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 74084–74086, 276710; FMNH 87251; MUSM 23823; UF 30447.

Additionally, although we have not seen the type (in Vienna: NMW B-921), the dorsal pelage of *M. macrura* appears to be distinctly more reddish than that of our vouchers based on photographs of NMW B-921 and a description of recently collected topotypes (incorrectly referred to as paratypes) in Miranda et al.'s (2021) report. Unfortunately, no other name appears to be available for our specimens, and as we are not prepared to describe a new species (relevant comparative material is widely scattered among Brazilian, North American, and European museums), our only recourse is to use Miranda et al.'s informal taxonomic notation.

ETHNOBIOLOGY: The Matses have no special name for this species.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: All four specimens of *Makalata* "species 5" accompanied by capture data from our region were shot or harpooned at night from trees at or near the edges of lakes or rivers in primary floodplain (seasonally inundated) forest. Seasonally flooded forest (either *igapó* or *várzea*) appear to be the predominant habitat of *Makalata* throughout its Amazonian distribution (Emmons, 1997; Patton et al., 2000; Miranda et al., 2022).

Mesomys hispidus (Desmarest, 1817)

Figure 52

VOUCHER MATERIAL (N = 9): Nuevo San Juan (AMNH 268252, 268269, 273080; MUSM 13306, 15328, 15329), San Pedro (MUSM 22346, UF 30599), Santa Cecilia (FMNH 87242).

UNVOUCHERED OBSERVATIONS: None.

IDENTIFICATION: Like other species of *Mesomys* (see below), the specimens that we refer to
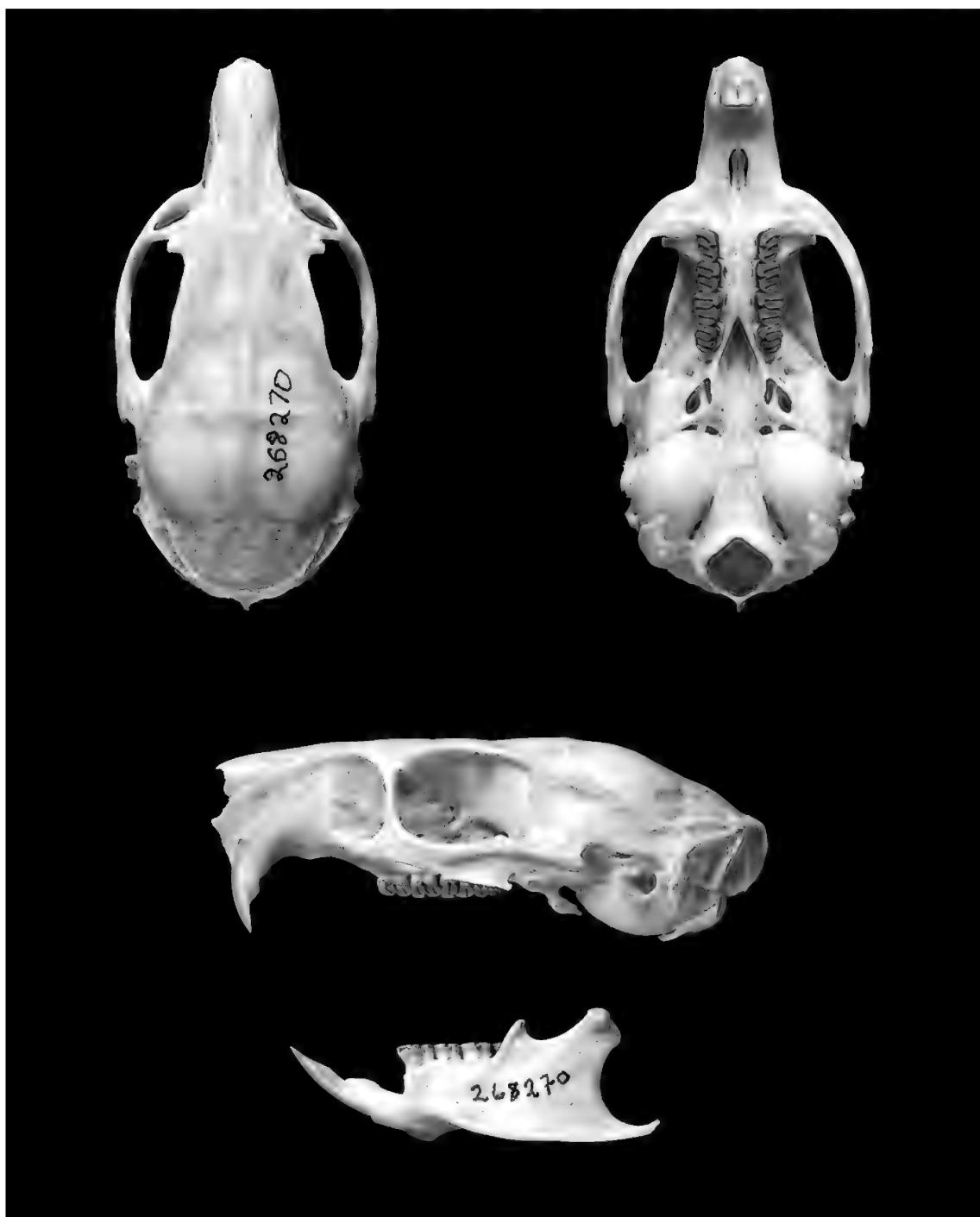
FIG. 51. Dorsal, ventral, and lateral cranial views of *Makalata* "species 5" (AMNH 268270). All views about ×1.6.

M. hispidus are small echimyines (HBL <200 mm) with conspicuously spiny, uniformly grizzled-brownish dorsal pelage and a sparsely haired tail with an obvious terminal tuft. The forefeet are mesaxonic (digits III and IV are equal in length), and manual digits II–V have strong, sharp claws. The upper cheektooth rows are approximately parallel (not strongly convergent anteriorly), and the upper cheekteeth (unlike those of other echimyines in our region) have closed labial flexi that are isolated as enamel islands on the occlusal surface, being essentially similar in this respect to the cheekteeth of *Proechimys*.

As currently recognized, *Mesomys hispidus* is a widespread Amazonian species that exhibits substantial geographic variation in size and mtDNA sequence characteristics (Patton et al., 2000; Orlando et al., 2003; Patton and Emmons, 2015b). Phylogenetic analyses of cytochrome *b* sequence data obtained from two of our vouchers (MUSM 13306, 22346) recovered both as members of "Clade A," a strongly supported haplogroup that included other sequences from eastern Peru and western Brazil (Orlando et al., 2003).[37] By contrast, a cytochrome *b* sequence obtained by the same authors from Desmarest's centuries-old holotype (MNHN 1998-2075) was recovered within "Clade F," a haplogroup composed of sequences from French Guiana that differ from those in Clade A by about 7% in model-corrected (K2P) comparisons. Among other evidence of phenotypic divergence between these lineages, the maxillary toothrow length of specimens in Clade A is 7.3 ± 0.2 mm, whereas the maxillary toothrow of specimens in Clade F is 6.2 ± 0.2 mm (Orlando et al., 2003: table 2). Measurements of our specimens (table 37) broadly overlap those of others assigned to Clade A (e.g., the "upriver clade" of Patton et al., 2000:

table 58), which they likewise resemble in qualitative traits.

The oldest available junior synonym of *Mesomys hispidus* (sensu Patton and Emmons, 2015b) with a type locality adjacent to the known range of Clade A is *ferrugineus* Günther, 1876, the description of which was based on a specimen collected about 240 km west of our region at Chamicuros (on the lower Río Huallaga at 5°30′S, 75°44′W; Moncrieff et al., 2019). On a 1998 visit to London, R.S.V. measured Günther's damaged type (BMNH 69.3.31.8), the intact dimensions of which (LD, 9.0 mm; MTR, 7.5 mm; LIB, 10.8 mm; ZB, 22.6 mm) are all within the range of morphometric variation in Clade A as documented in the references cited above. Although Thomas (1911: 607) thought that Günther's *ferrugineus* "cannot be separated" from *ecaudatus* Wagner, 1845 (another junior synonym of *M. hispidus* as currently recognized), the type locality of *ecaudatus* (Borba, at 4°24′S, 59°35′W, on the right bank of the lower Rio Madeira; Paynter and Traylor, 1991) is over 1000 km distant from the known range of Clade A, and it is on the opposite side of a known biogeographic barrier.

Thus, *Mesomys ferrugineus* would seem to be the appropriate name for Clade A (including our specimens from the Yavari-Ucayali interfluve) if additional taxa were to be recognized as valid within the *M. hispidus* complex. As others before us (e.g., Orlando et al., 2003) have concluded, however, it seems prudent to await additional analyses based on nuclear loci, karyotypes, and more densely sampled phenotypic data before disrupting the taxonomic status quo.

ETHNOBIOLOGY: The Matses have no special name for this species.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: Six specimens of *Mesomys hispidus* are accompanied by habitat information from our region. Of these, one dropped from a tree that was being felled for a new swidden in primary upland forest, four were shot at night from trees in primary floodplain (seasonally inundated) forest,

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[37] In Orlando et al.'s (2003: fig. 2) phylogeny MUSM 13306 was mislabelled as having come from Cusco department, although its correct provenance was given in one of their appendices (Orlando et al., 2003: 120). The sequence that they identified as MV970002 (Michael Valqui's field number) corresponds to the specimen now cataloged as MUSM 22346.
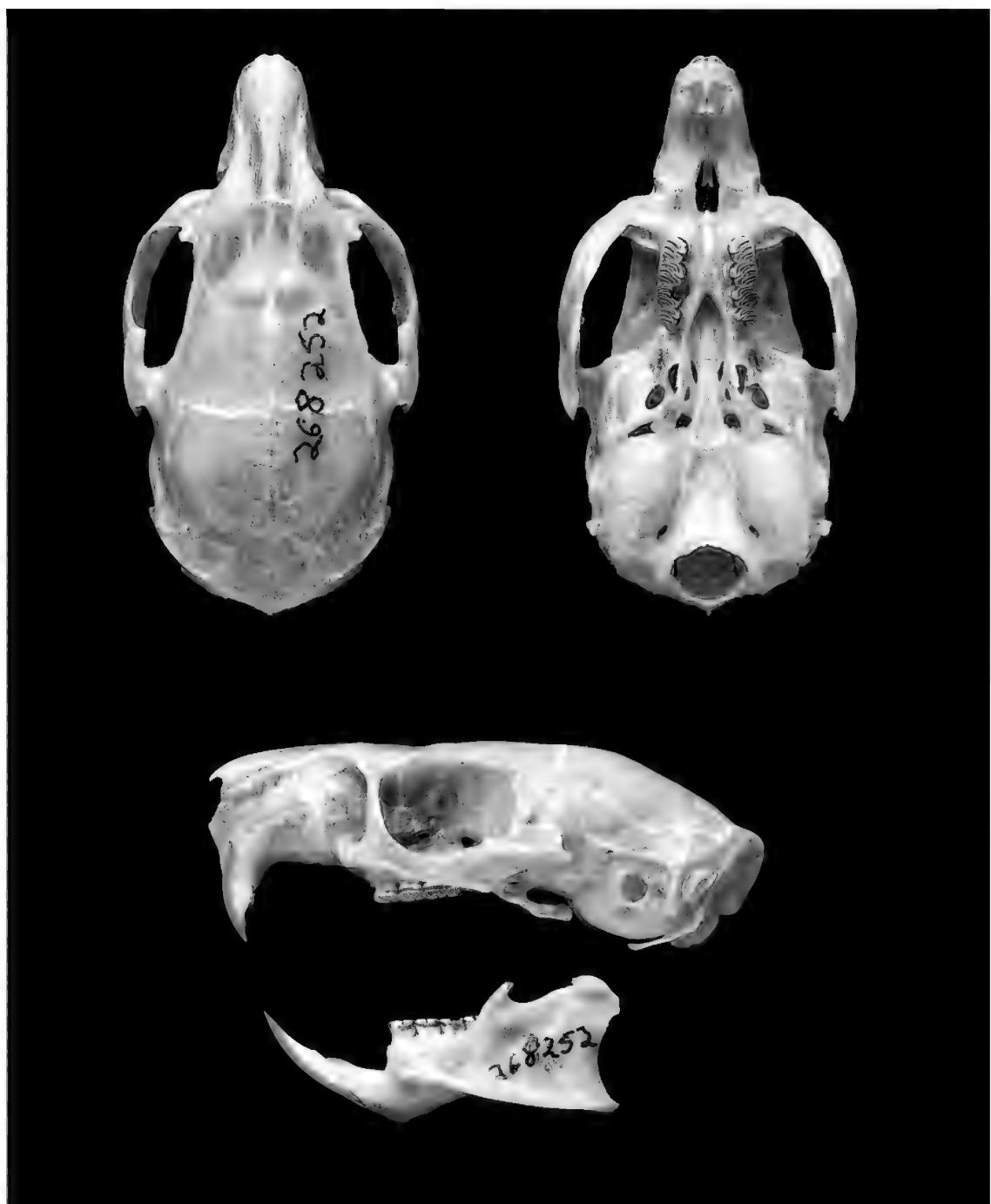
FIG. 52. Dorsal, ventral, and lateral cranial views of *Mesomys hispidus* (AMNH 668252). All views about ×1.8.

and one was trapped on a liana in open hillcrest forest. Recorded heights from which specimens were shot or trapped ranged from 1 to 10 m above the ground. Sparse as they are, these data are consistent with observations previously summarized by Emmons (1997) and Patton et al. (2000) that *M. hispidus* is a eurytopic arboreal species.

Toromys rhipidurus (Thomas, 1928)

Figure 53

VOUCHER MATERIAL (N = 10): Amelia (FMNH 19854), Jenaro Herrera (AMNH 276710, MUSM 23823), Orosa (AMNH 74084–74086), Santa Cecilia (FMNH 87250–87252), San Pedro (UF 30447).

UNVOUCHERED OBSERVATIONS: Apparently none.

IDENTIFICATION: *Toromys rhipidurus* has spiny fur, but because the spines have soft tips, they do not feel sharp. The dorsal pelage is coarsely grizzled brownish, but the nose and (sometimes) the rump and tail base are reddish; the ventral fur is gray-based beige and does not contrast sharply in color with the back and sides. The tail is distinctively blackish in recently collected specimens, and it is densely covered with straight, stiff hairs that almost, but do not quite conceal the underlying scales. In these and other morphological details (including external and craniodental measurements; table 37), our voucher material fits the authoritative description of *T. rhipidurus* in Emmons and Fabre (2018: 38–39).[38]

ETHNOBIOLOGY: The Matses have no special name for this species.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: The two specimens of *Toromys rhipidurus* from Jenaro Herrera were taken in seasonally flooded forest in the Río Ucayali floodplain. The only other specimen from our region accompanied by habitat information (UF 30447) was taken in "riverine vegetation" according

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[38] An earlier description of *Toromys rhipidurus* (Emmons et al., 2015c: 930–931) was based on material that included specimens of *T. albiventris* Emmons and Fabre, 2018.

ing to the skin tag. This specimen might be one of the seven individuals that Valqui (2001) sighted along a 1 km stretch of flooded forest while travelling at night by canoe near San Pedro. These scant habitat indications are consistent with the observations of Colombian researchers (Lozano-Flórez and Cifuentes-Acevedo, 2020) that this species inhabits riparian (*várzea* and/or *igapó*) forest.

Terrestrial Echimyids (Myocastorini)

The terrestrial echimyids in our region are all members of the genus *Proechimys* J.A. Allen, 1899, commonly known as spiny rats. These are among the commonest—or at least the most frequently trapped—terrestrial rodents everywhere in Amazonia. Spiny rats differ from sympatric arboreal echimyids by their shorter tails (less than the combined length of the head and body), which are always bicolored (dark dorsally and abruptly paler ventrally) and lack terminal tufts of long apical hairs. Additionally, species of *Proechimys* have mesaxonic forefeet (with digit III longer than digit IV) and long, narrow hind feet with short outer digits (the claw of dI never extends even half the length of the first phalange of dII, and the claw of dV does not extend to the end of the first phalange of dIV). The dorsal pelage is always some shade of brown, and these drab rats entirely lack facial stripes, reddish noses, reddish rumps, or any other distinctive markings. The upper cheekteeth have a single lingual fold that never extends more than halfway across the crown. Several labial folds ("counterfolds" sensu Moojen, 1948) are patent in very young animals but become isolated as internal enamel islands with advancing toothwear.

Seven strongly supported and highly divergent mtDNA lineages are represented among the 38 cytochrome *b* sequences we analyzed from *Proechimys* specimens collected in the Yavarí-Ucayali interfluve (fig. 54, table 38, appendix 4). Based on morphological character data (table 39), we associate these seven lineages with six taxa currently recognized as valid
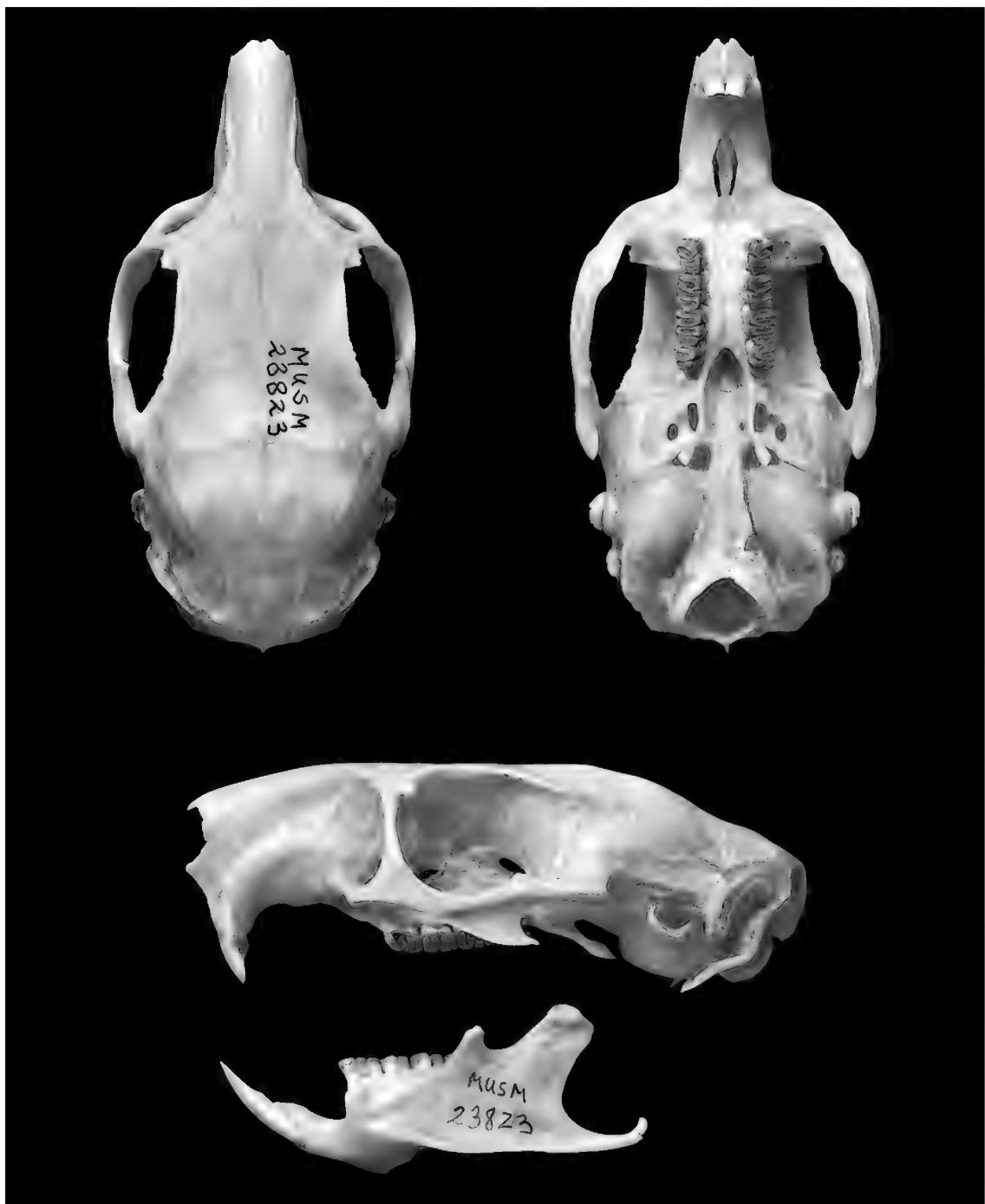
FIG. 53. Dorsal, ventral, and lateral cranial views of *Toromys rhipidurus* (MUSM 23823). All views about ×1.6.
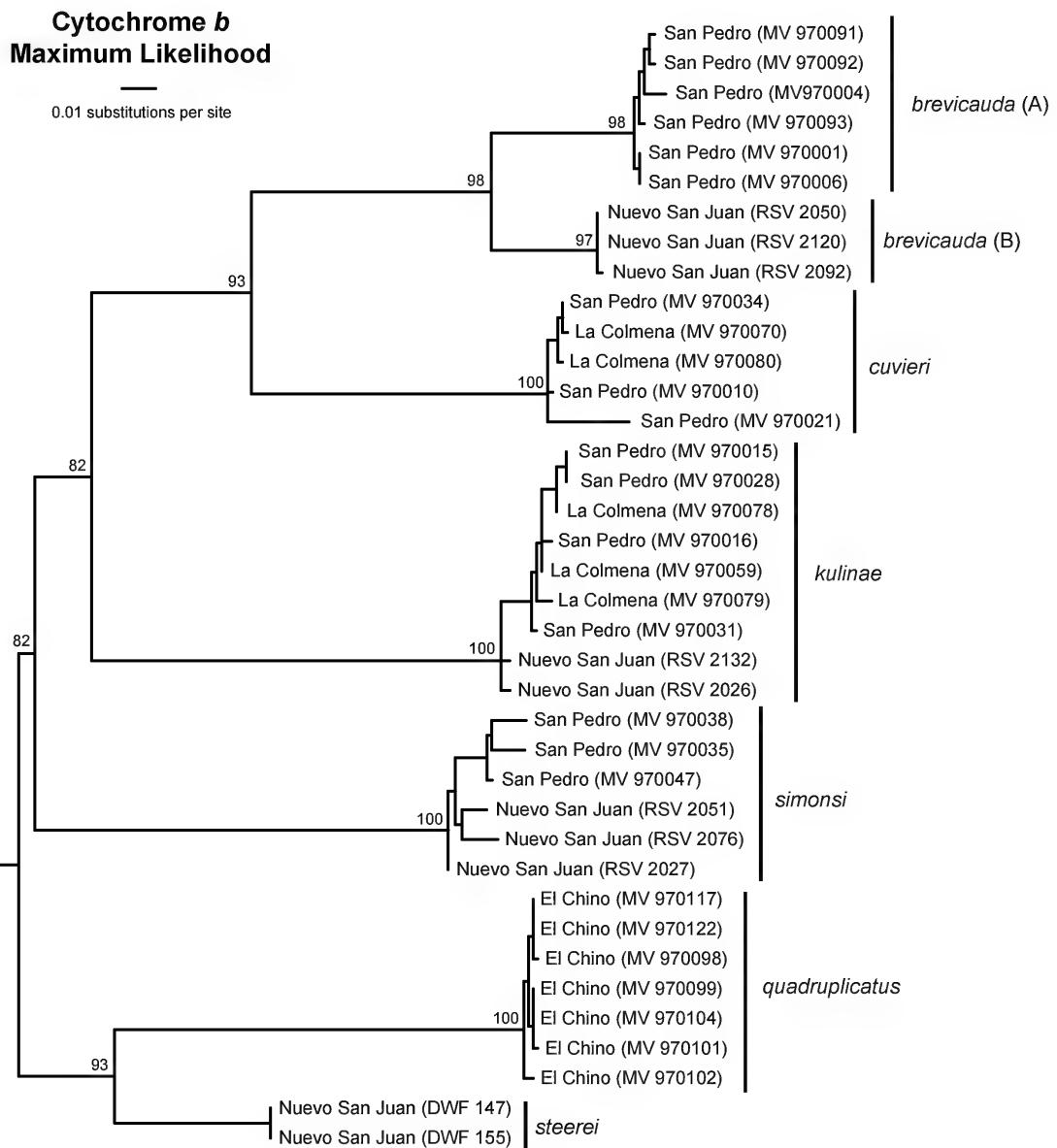
FIG. 54. Maximum-likelihood topology for cytochrome *b* sequences of 38 *Proechimys* specimens collected in the Yavarí-Ucayali interfluve. Bootstrap support values are provided above selected branches. The outgroup (*Hoplomys gymnurus*; see Materials and Methods) is not shown. Terminals are labeled with locality names (appendix 1) and field numbers of sequenced specimens (appendix 4).

TABLE 38

Average Percent Uncorrected Cytochrome *b* Sequence Divergence within and among Species of *Proechimys* from the Yavarí-Ucayali Interfluve

	brevicauda	cuvieri	kulinae	quadruplicatus	simonsi	steerei
brevicauda	**3.30**					
cuvieri	11.77	**1.24**				
kulinae	13.76	12.52	**0.91**			
quadruplicatus	13.69	13.73	13.43	**0.35**		
simonsi	13.58	15.21	13.53	14.83	**1.89**	
steerei	13.52	12.95	11.84	11.12	12.43	**0.00**

species. Of these, *P. brevicauda* and *P. cuvieri* belong to the Longicaudatus Group of Patton and Leite (2015), *P. kulinae* belongs to their Gardneri Group, *P. quadruplicatus* and *P. steerei* belong to their Goeldii Group, and *P. simonsi* belongs to their Simonsi Group. Two strongly supported mtDNA sister lineages share the morphological phenotype that corresponds to *P. brevicauda*, an anomaly that we discuss in the account for that species. All our taxonomic identifications are consistent with the names suggested by Dalapicolla et al. (2024), who report a comprehensive molecular analysis of the genus that includes several sequences from specimens collected in our region.

Morphological characters: Species of *Proechimys* are difficult to distinguish in the field—hence our reluctance to accept unvouchered identifications (see below)—but most adult specimens can be confidently identified using a combination of pelage, craniodental, and bacular traits (Patton, 1987; Patton et al., 2000; Patton and Leite, 2015). Although taxonomic differences in spine morphology, ear size, tail length, tail scales, tail coloration, and the number of plantar pads on the hind foot have been described by authors, we were unable to consistently distinguish species in our region by such criteria. Similarly, although the literature often mentions subtle species differences in cranial shape, the species in our region are so similar in this respect as to be effectively indistinguishable. By contrast, the following craniodental characters were

among the most consistently useful of those we surveyed while attempting to identify material from the Yavarí-Ucayali interfluve, including 239 UF specimens collected by Michael Valqui at various localities along the Río Tahuayo and the Quebrada Blanco.[39]

1. The incisive foramina exhibit considerable taxonomic variation. In several species (e.g., *Proechimys brevicauda*, *P. cuvieri*) the foramina are said to be lyre shaped or lyrate because they are abruptly constricted posteriorly by lateral flanges of bone (Patton, 1987: figs. 13a, 13b, 14c). Alternatively, these foramina can be more or less oval, with rounded outer margins and lacking abrupt posterolateral constrictions (e.g., in most specimens of *P. simonsi*; Patton, 1987: fig. 17a, 17d). Lastly, these foramina can have parallel or subparallel lateral margins (e.g., in most specimens of *P. kulinae*). However, intermediate morphologies also exist, with the result that foraminal shape is sometimes hard to categorize, necessitating the use of modifiers (such as "weakly lyrate," etc.).

2. The bony septum that divides the left and right incisive foramina is another source of taxonomically useful traits. This septum consists of three elements contributed by the premaxillary, vomer, and maxillary bones. In some species (e.g., *Proechimys simonsi*; Patton, 1987: fig. 17b,

[39] Only 17 specimens (about 7%) of this important series were misidentified, a modest error rate that lends some confidence to habitat attributions in the text of Valqui's (2001) thesis (as quoted in the following accounts).

17c), the premaxillary septum is usually short, not extending posteriorly much beyond the middle of the foramina, but in others (e.g., *P. brevicaudata* and *P. cuvieri*; Patton, 1987: figs. 13, 14) it is substantially longer. The vomer (which forms a capsule around Jacobson's organ) is usually concealed within the premaxillary septum of some species (e.g., *P. steerei*; Patton, 1987: fig. 15), but it is often exposed to ventral view in others (e.g., *P. brevicaudata* and *P. cuvieri*; Patton, 1987: figs. 13, 14). The most posterior part of the incisive septum, formed by the maxillary bones, varies greatly in size and shape. Whereas the maxillary septum is short in some species (e.g., *P. simonsi*; Patton, 1987: fig. 17), it is often longer in others (e.g., *P. steerei*; Patton, 1987: fig. 15c, 15d); additionally, the maxillary septum often forms a prominent sagittal keel in some species (e.g., *P. brevicauda*; Patton, 1987: fig. 13b), but not in others. Finally, whereas the incisive septum completely separates the left and right foramina in many species, it is often incomplete in others (e.g., *P. simonsi*; Patton, 1987: figs. 17c, 17d).

3. The anterior postdiastemal palate (hereafter, the anterior palate: between the left and right upper premolars) is marked by shallow but distinct lateral grooves and a median ridge in some taxa (e.g., *Proechimys brevicauda*; Patton, 1987: fig. 13), but not in others (e.g., *P. simonsi*; Patton, 1987; fig.17). Although prominently grooved-and-ridged anterior palates are only observed in taxa with lyrate incisive foramina, not all species with lyrate incisive foramina have grooved-and-ridged anterior palates (e.g., *P. cuvieri*; Patton, 1987: fig. 14).

4. The floor of the infraorbital foramen is usually smooth and devoid of prominent relief in some taxa (e.g., *Proechimys cuvieri*; Voss et al., 2001: fig. 78A), but a distinct bony ridge often defines the lateral margin of an open canal for the infraorbital nerve in others (e.g., the extralimital species *P. guyannensis*; Voss et al., 2001: 78C). We scored this variation following Patton (1987): canal absent (no lateral ridge, score = 1); canal present (distinct lateral ridge, score = 2).

Following Patton's scoring convention, we recorded intermediate conditions as decimal fractions (e.g., 1.5).

5. The mesopterygoid fossa penetrates between the molar rows to a taxonomically variable extent. Following Patton (1987) we scored mesopterygoid penetration as follows: mesopterygoid fossa extends to but not between M3s (score = 1), mesopterygoid fossa extends between M3 hypocones (score = 2), mesopterygoid fossa extends between M3 protocones (score = 3), mesopterygoid fossa extends between M2 hypocones (score = 4). Laying a straightedge tangent to the anterior margin of the mesopterygoid fossa is helpful for judging penetration between dental landmarks.

6. The supraorbital crest is continuous with a bony shelf on the anterolateral braincase that extends posteriorly to a point just above the squamosal root of the zygomatic arch. This shelf, the temporal crest, terminates at or near the squamosal-parietal suture in some species (e.g., *P. cuvieri*), but in others the temporal crest extends onto the parietal. We recorded the parietal extension of the temporal crest as "short" if it does not extend above the postglenoid foramen or "long" if it extends above or beyond the postglenoid foramen. The only species that usually has a long parietal extension of the temporal crest in our region is *P. kulinae*.

7. The cheekteeth (dP4–M3) usually have only three labial folds ("counterfolds" sensu Moojen, 1948) in some species (e.g., *Proechimys brevicauda*, *P. simonsi*), but other species (e.g., *P. quadruplicatus*) usually have four labial folds on one or more teeth. Although counting enamel folds sounds straightforward, some care is needed in assessing taxonomic differences in this trait. Because the posteriormost (fourth) labial fold—when present—is shallower than the first three folds, it is often lost in older specimens with heavily worn teeth. Also, in species with four folds on each unworn cheektooth, the fourth fold is lost first on the more anterior teeth, which are the earliest to erupt and therefore get worn down sooner than the more posterior teeth. Following Patton and Leite (2015), we

TABLE 39

Selected External and Craniodental Differences among Species of *Proechimys* from the Yavari-Ucayali Interfluve

	P. brevicauda	*P. cuvieri*	*P. kulinae*	*P. quadruplicatus*	*P. simonsi*	*P. steerei*
Hind foot (length)	42–50 mm	45–53 mm	37–44 mm	48–57 mm	43–53 mm	52–57 mm
Ventral pelage (color)	whitish marked with pale brown on throat & often elsewhere	usually white, but sometimes marked with pale brown	pure white	pure white	pure white	pure white
Ventral pelage (texture)	thin & mostly spiny	thin & mostly spiny	thin & mostly spiny	thin & mostly spiny	thin & mostly spiny	denser & woolier
Baculum (width/length)	0.40–0.49	0.74–1.18	0.26–0.37	0.33–0.37	0.16–0.25	0.22–0.32
Baculum (apical processes)	present, short	present, long	indistinct	indistinct	indistinct	indistinct
Incisive foramen shape	lyrate	lyrate	usually oval or parallel	usually lyrate	usually oval	lyrate
Incisive septum	complete	complete	usually complete	often incomplete	often incomplete	complete
Premaxillary portion	long	long	usually short	usually short	usually short	short
Vomerine capsule	exposed	often exposed	usually concealed	usually concealed	usually concealed	usually concealed
Maxillary portion	short & usually strongly keeled	short & usually not keeled	usually weakly keeled	often very long & weakly keeled	usually short & not or weakly keeled	very long & keeled
Anterior palate	grooved	usually not grooved	not or weakly grooved	usually not grooved or weakly grooved	not grooved	grooved
IOF floor	smooth	usually smooth	usually smooth	with or without nerve canal	usually with deep nerve canal	with weakly defined nerve canal
Mesopterygoid fossa score	2.1 (1–3)	2.5 (2–3)	3.5 (3–4)	2.8 (2–4)	3.4 (3–4)	2.2 (1–3)
Maxillary toothrow length	8.2–9.1 mm	8.3–9.2 mm	7.1–7.5 mm	8.6–9.6 mm	7.7–9.3 mm	8.4–9.6
Temporal crest on parietal	absent/ indistinct	usually absent	usually long	often long	absent or short	absent or short
Labial folds (dP4–M3)	3-3-3-3	3-3-4(3)-3(4)	3-3-3-3(2)	4-4-4(3)-4(3)	3-3-3(4)-3(4)	3-3-4(3)-3

recorded the number of labial folds on successive teeth as counts punctuated by hyphens: thus, 3-3-3-3 for a specimen with three labial folds each on dP4–M3. Summary formulae for samples express observed intraspecific variation by placing the least frequent variant in parentheses: thus, 3-3-3(4)-3 for a sample in which most individuals have three labial folds on each tooth, but in which some have four folds on M2.

Ethnobiology: Spiny rats are called tambisëmpi (literally "little pacas"), but this term is also used in a general sense to include all rats and mice (Echimyidae and Cricetidae). The only archaic synonym is madempi (made is an archaic name for paca), although this term refers only to spiny rats and is not synonymous with the more general meaning of tambisëmpi. The Matses recognize variation among spiny rats in size, coloration, and the presence or absence of tails (easily detached and often healed in Proechimys spp.), but they do not distinguish these variants linguistically.

Spiny rats are a minor game species due to their small size. Despite being smaller than acouchies, they are a more important food source, since many can be killed in a single night by trapping. Spiny rats are trapped using deadfall traps baited with manioc (fig. 55). A line of 10 to 20 traps is typically constructed around the edge of a swidden when it is discovered that spiny rats are eating manioc tubers. Adults and/or children build and check the traps. The traps are built right at the edge of the swidden where spiny rat paths are detected. It is not uncommon for half of the traps to kill spiny rats on the first night after traps are built. Thereafter the number of nightly kills decreases until only one or none is killed, at which point the Matses stop baiting the traps. Such traps can be repaired and baited again after several months. Additionally, children often build deadfall traps in secondary forest.

Spiny rat burrows are sometimes discovered in the forest by hunters or by women. The hunter first pokes a stick into the burrow, and if spiny rat hairs are stuck to the end of the stick, he knows the burrow is inhabited. Then he builds a small fire at the burrow entrance, plaits a fire-fan from the leaflets of a new pinchuk palm (Astrocaryum murumuru) frond, and fans the smoke into the burrow. When the rat comes out, the hunter grabs it with his hands. If he is not carrying implements for starting a fire, he will dig out the burrow to catch the spiny rat.

Spiny rats are also sometimes captured by hand when their brush nests are disturbed as undergrowth is being cleared in preparation for felling a swidden.

Typically eaten for breakfast, spiny rats are prepared for cooking by singeing off the fur, after which they are gutted and roasted. No dietary taboos are associated with spiny rats.

Matses natural history: Spiny rats are reddish with a white venter. They have a long tail that they drag as they walk. Some do not have a tail. They have spines on their backs. Males have large testicles. They get very fat during the rainy season.

Spiny rats are found in primary and secondary forest, but they are more abundant in secondary forest, especially near Matses swiddens. They are the most abundant type of rat/mouse.

Spiny rats dig burrows and line them with dry leaves. They also make nests in brush piles on the ground. They also live in hollow logs into which they carry many leaves.

Spiny rats are nocturnal. They make paths, which often go under ferns, which hide the path.

Spiny rats are solitary, except when they travel with their young following them. When two spiny rats meet each other, they "laugh" (vocalize) and then go their separate ways.

Spiny rats are eaten by ocelots, margays, jaguarundis, bush dogs, short-eared dogs, tayras, common opossums, and snakes.

The spiny rat says "cho cho cho" as it runs off when illuminated with a flashlight.

Spiny rats eat dicot tree fruits and the mesocarp of swamp-palm (Mauritia flexuosa) and isan palm (Oenocarpus bataua) fruits. In Matses swiddens they eat manioc, plantains, and maize. They come to where the Matses throw out trash to eat bits of manioc, manioc peels, etc.
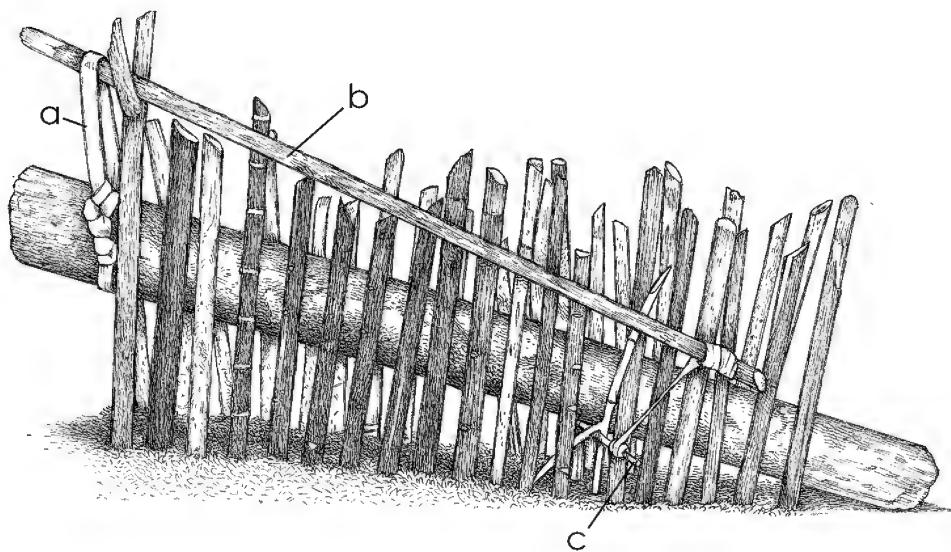
FIG. 55. A deadfall trap constructed by the Matses to kill *Proechimys* spp. (Photo by D.W.F., drawing by Patricia J. Wynne). A heavy log, closely fenced on both sides by stakes thrust into the ground, is suspended by a bark strap (a) from a long lever (b) secured to a trigger stick (c) at its opposite end. The bait consists of an upright piece of manioc root wedged between the ground and the inner end of the trigger stick.

REMARKS: Matses observations about *Proechimys* are consistent with a large scientific literature (succinctly summarized by Emmons, 1997) on these numerically abundant nocturnal, terrestrial rats.

Proechimys brevicauda (Günther, 1876)

Figures 56A, 56D

VOUCHER MATERIAL (*N* = 27): Nuevo San Juan (AMNH 268273, 268275, 268276, 268281, 268282, 272698, 272700; MUSM 11258, 11262, 11297, 11298, 11316, 13337, 13338), San Fernando (FMNH 88959), San Pedro (MVZ 198475; UF 30548–30550, 30552–30555, 30603, 30637, 30713), Siete de Julio (UF 30775). Pacheco (1991) and Pavlinov (1994) also recorded this species from Jenaro Herrera based on collected material (at the ZMMU and MUSM, respectively) that we have not seen.

UNVOUCHERED OBSERVATIONS: Field identifications of this species cannot be accepted as valid without supporting voucher material.

IDENTIFICATION: *Proechimys brevicauda* is a medium-sized species that, in our region, has dark-brownish dorsal fur and ventral fur that is often mottled with buff or pale-brown markings; one specimen (UF 30549), however, has almost entirely pale-brown ventral fur, with whitish blotches only on the chest and inguinal region. Brownish ventral markings are especially seen on the throat, which is not pure white in any specimen we examined. Even in specimens with mostly whitish ventral fur, the color transition to the dorsal fur tends to be less abrupt than in most other species (e.g., *P. kulinae*, *P. simonsi*, *P. steerei*) because there is often a lateral line of buff or pale-brown fur. The ventral fur is thin and feels harsh to the touch because it consists mostly of soft spines with only a few wool hairs mixed among them. The hind feet appear darker than in most other sympatric species because the pedal fur is brownish (pale brown in some specimens, but never pure white).

The baculum (which we examined from five specimens) is about 9.6 mm long and about 4.0 mm wide proximally, on average, with short but well-developed apical processes and an average width-to-length ratio of 0.47 (range = 0.40–0.49).

Distinctive craniodental features of this species include consistently lyrate (but sometimes only weakly lyrate) incisive foramina from which more or less distinct lateral grooves extend posteriorly onto the anterior palate, which also exhibits a median ridge. The incisive septum is always complete in the specimens we examined, with a long premaxillary portion and a maxillary process that is often strongly keeled. The vomer is broadly exposed in most specimens. The mesopterygoid fossa usually penetrates between the third molars, but not as deeply as in other species (mean score for this character = 2.1, range = 1–3). The floor of the infraorbital foramen is almost always smooth, the temporal crest lacks a distinct parietal extension, and there are only three labial folds on all the upper cheekteeth (3-3-3-3) in the specimens we examined.

The phenotype we identify as *Proechimys brevicauda* closely resembles Patton and Leite's (2015: 971–972) description with the noteworthy exceptions that (1) none of our specimens could really be described as reddish brown, (2) the mesopterygoid fossa penetrates between the third molars in most of our specimens, and (3) none of our specimens has a well-developed parietal extension of the temporal crest. Despite such discrepancies—and a few others involving morphological traits we did not score for analysis—phylogenetic analyses of DNA sequence data obtained from three specimens collected in our region (AMNH 272698, 272700; MUSM 13338) recovered them as members of the same molecular clade previously associated with this name (Dalapicolla et al., 2024: appendix E, fig. S4). Measurements of our material (table 40) broadly overlap those of Patton et al.'s (2000: table 64) series from the Rio Juruá.
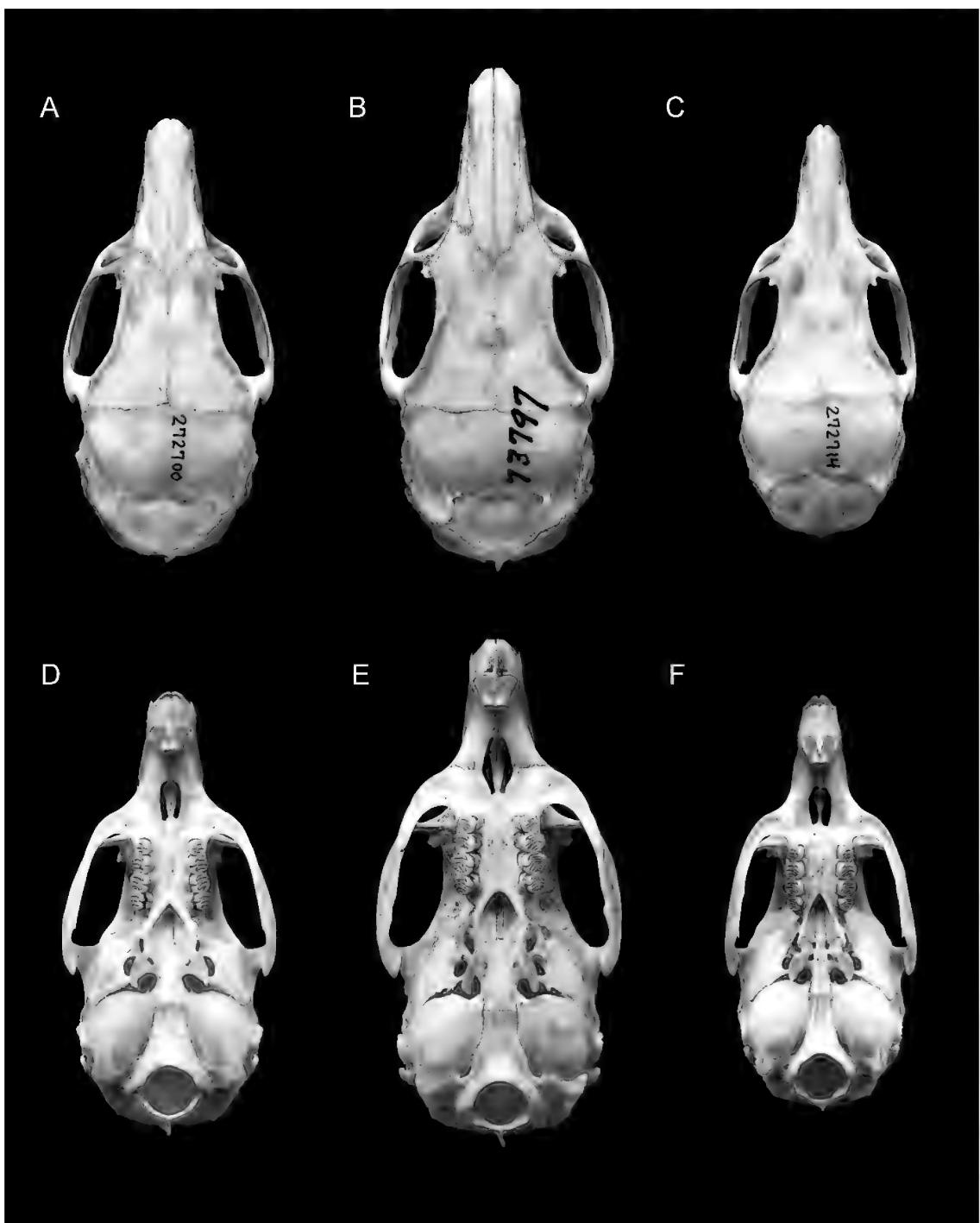
FIG. 56. Dorsal and ventral cranial views of *Proechimys brevicauda* (**A**, **D**; AMNH 272700), *P. cuvieri* (**B**, **E**; AMNH 73797), and *P. kulinae* (**C**, **F**; AMNH 272714). All views about ×1.3.

TABLE 40

External and Craniodental Measurements (mm) and Weights (g) of *Proechimys brevicauda*, *P. cuvieri*, and *P. kulinae* from the Yavarí-Ucayali Interfluvial Region

	P. brevicauda[a]	*P. cuvieri*[b]	*P. kulinae*[c]
HBL	215 ± 11 (201–234) 11	224 ± 17 (207–245) 5	183 ± 12 (159–201) 15
LT	133 ± 13 (110–150) 9	149 ± 18 (123–166) 4	125 ± 13 (110–155) 15
HF	46 ± 3 (42–50) 12	49 ± 2 (45–53) 16	40 ± 2 (37–44) 22
Ear	21 ± 1 (20–21) 11	21 ± 2 (18–23) 5	21 ± 2 (17–24) 19
CIL	44.5 ± 2.3 (40.9–46.9) 9	46.1 ± 2.6 (41.9–50.0) 14	38.5 ± 1.5 (35.0–41.0) 22
LD	11.3 ± 0.9 (10.0–12.3) 11	12.0 ± 0.9 (10.6–13.6) 17	9.7 ± 0.5 (8.7–10.5) 24
MTR	8.6 ± 0.3 (8.2–9.1) 11	8.8 ± 0.3 (8.3–9.4) 17	7.2 ± 0.2 (6.7–7.7) 24
LIF	5.4 ± 0.8 (4.1–6.4) 11	5.9 ± 0.5 (5.1–7.2) 17	4.1 ± 0.4 (3.2–5.2) 24
BIF	2.8 ± 0.4 (2.2–3.3) 10	3.0 ± 0.3 (2.3–3.4) 17	2.3 ± 0.2 (1.8–2.7) 24
LN	20.3 ± 1.5 (17.4–21.8) 10	21.1 ± 1.5 (18.6–23.6) 17	17.5 ± 0.9 (15.7–19.4) 22
LIB	11.7 ± 0.8 (10.8–13.0) 11	12.3 ± 0.6 (11.5–13.5) 16	10.0 ± 0.5 (9.0–11.3) 24
ZL	17.4 ± 1.0 (16.3–19.0) 11	17.5 ± 1.8 (11.7–20.2) 17	15.4 ± 0.7 (13.6–16.7) 23
ZB	25.2 ± 0.9 (23.7–26.3) 10	26.7 ± 1.2 (24.5–28.6) 14	22.2 ± 1.0 (20.3–23.4) 23
Weight	307 ± 53 (205–361) 12	356 ± 66 (256–445) 6	180 ± 24 (135–223) 23

[a] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 268273, 268275, 268276, 268281, 268282, 272700; MUSM 11258, 11262, 11297; MVZ 198475; UF 30549, 30553.

[b] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 73792, 73793, 73795–73798, 73800, 74090, 74092, 74094; UF 30561, 30572, 30576.

[c] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 272714, 276707, 276708; MUSM 11300, 23826, 23832; MVZ 198489; UF 30551, 30597, 30607, 30613, 30622, 30624, 30648, 30650, 30662, 30675–30677, 30680, 30684, 30705, 30706, 30714.

The two haplogroups found in our region (fig. 54) are morphologically indistinguishable based on the specimens we examined; both correspond to *Proechimys brevicauda* as diagnosed in this report, but it is possible that they represent cryptic taxa. The sequences from San Pedro ("*brevicauda* A") differ from Nuevo San Juan sequences ("*brevicauda* B") by 6.1% (uncorrected), a very large value for samples collected only 100 km apart in the same interfluvial region. Because *P. brevicauda* is based on a specimen from Loreto,[40] it is likely that this name properly applies to at least one of our local haplogroups, should they eventually prove to be valid species. Among the nominal taxa currently treated as junior synonyms of *P. brevicauda*, the closest to our region is *gularis* Thomas, 1911 (based on a type from eastern Ecuador), but Patton and Leite (2015) listed others from southern Peru and eastern Bolivia. Our observation of near-sympatry between substantially divergent haplogroups of this species is another example of the genetic heterogeneity previously discussed by Patton et al. (2000: 213–224).

ETHNOBIOLOGY: The Matses have no special name for this species.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: Twelve specimens of *Proechimys brevicauda* are accompanied by habitat informa-

[40] The lectotype (BMNH 69.3.31.7; designated by Thomas, 1900b) was collected by Edward Bartlett in 1867 or 1868 at Chamicuros, a locality that is sometimes said to have been on the upper Río Samiria (Stephens and Traylor, 1983), but which was probably on the lower Huallaga at or near 5°30′S, 75°44′W (Moncrieff et al., 2019).

tion from our region.[41] Of these, six were trapped in primary upland forest (in densely vegetated valley bottoms and on open hillsides), four were trapped in secondary growth, and two were trapped in swiddens; all recorded captures were made in traps set on the ground. According to Valqui (2001)—most of whose voucher specimens (at the UF) were correctly identified—this species was uncommon at San Pedro, where it was found "mainly around houses, fields, and in secondary forests of the terra firme ... only two specimens were obtained in hills or plateaus covered with primary forests."

Proechimys cuvieri Petter, 1978

Figures 56B, 56E

VOUCHER MATERIAL (*N* = 38): Nuevo San Juan (MUSM 11259, 11263, 11266, 11271, 11308, 11309), Orosa (AMNH 73792–73800, 74089–74092), San Pedro (UF 30558, 30559, 30561, 30563, 30565, 30567–30572, 30574, 30577, 30788; MVZ 198511), Siete de Julio (30576, 30780, 30782, 30783).

UNVOUCHERED OBSERVATIONS: Field identifications of this species cannot be accepted as valid without supporting voucher material.

IDENTIFICATION: *Proechimys cuvieri* is another medium-sized species, indistinguishable in external and craniodental dimensions from *P. brevicauda* (table 40), which it likewise resembles in most qualitative morphological traits. The dorsal pelage is brownish—like the dorsal pelage of most sympatric congeners (*P. steerei*, with distinctively reddish-brown dorsal pelage, is the unique exception; see below)—but in side by side comparisons it appears more coarsely grizzled and has broader and stiffer spines than those of *P. brevicauda*. The ventral pelage is entirely white

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[41] Despite the abundance of *Proechimys* species in our region, ecological information summarized in these accounts is limited because many MUSM specimens were preserved in fluid, and their skulls have yet to be extracted and cleaned; these specimens could not be confidently identified to species, nor were we able to confidently identify all juvenile specimens among those with cleaned cranial material.

in some specimens (e.g., AMNH 74090, MUSM 11263), but it is marked with pale brown—especially on the throat and laterally—in others (AMNH 73797, 73798, 73800). The ventral fur is thin and feels harsh to the touch because it consists mostly of soft spines with only a few wool hairs mixed among them. Most specimens have brownish dorsal fur on the hind feet, which do not differ conspicuously in coloration from those of *P. brevicauda* based on the material we examined. By contrast, the baculum (which we examined from eight specimens) is diagnostically short (6.8 mm, on average), broad (5.7 mm proximally), and deeply forked (Patton et al., 2000: fig. 137), with an average ratio of basal width to length of about 0.94 (range = 0.74–1.18), quite unlike the bacular morphology of other spiny rats in our region.

Distinctive craniodental traits of *Proechimys cuvieri* include consistently strongly lyrate incisive foramina from which shallow grooves extend onto the posterior part of the diastema but usually not between the premolars, resulting in an ungrooved (or very weakly grooved) and usually ridgeless anterior palate. The incisive septum is complete, with a long premaxillary portion and a short maxillary portion that is not strongly keeled in any specimen we examined; the vomer is usually at least partially exposed. The mesopterygoid fossa always extends between the third molars, often deeply (mean score for this character = 2.5, range = 2–3). The floor of the infraorbital foramen is usually smooth (range of scores = 1–1.5), and the temporal crest usually lacks a distinct parietal extension, although more or less distinct extensions of variable length occur in a few specimens (e.g., AMNH 73796, 73797). The first two upper cheekteeth have only three labial folds, but M2 usually has four, and M3 sometimes also does, resulting in a sample formula of 3-3-4(3)-3(4).

Our specimens correspond closely to Patton and Leite's (2015: 974) qualitative description of *Proechimys cuvieri*, although the ventral pelage of our specimens (as previously noted) is sometimes marked with pale brown and the hind feet

are usually brownish, such that this species cannot be distinguished consistently from *P. brevicauda* based on pelage coloration, at least in our region. Additionally, whereas Patton and Leite describe this species as typically having three labial folds on each upper cheektooth, M2 usually—in 13 of 17 specimens we scored for this character—has four labial folds in our material.

Measurements of our series (table 40) closely resemble those of topotypical specimens of *Proechimys cuvieri* (from French Guiana; Voss et al., 2001: table 45) despite substantial mtDNA (cytochrome *b*) divergence among geographic populations of this widespread species (Patton and Leite, 2015) or species complex (Dalapicolla et al., 2024). Measurements of our series also resemble those of *P. cuvieri* from the Rio Juruá as reported by Patton et al. (2000: table 64), with the unique exception of mean condyloincisive length (CIL), for which Patton et al.'s sample differs from ours by more than two standard deviations, an obvious lapsus.[42] As previously noted by Voss et al. (2001), there are substantial differences in cranial trait frequencies among geographic populations of *P. cuvieri*, but morphological differences have yet to be convincingly correlated with mtDNA clade membership, so their taxonomic relevance is unclear.

ETHNOBIOLOGY: The Matses have no special name for this species.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: Six specimens of *Proechimys cuvieri* from Nuevo San Juan are accompanied by habitat information. Of these, three were trapped in upland primary forest and three were trapped in swiddens; all recorded captures were made in traps set on the ground. By contrast, the 13 specimens from Orosa were almost

certainly taken in *várzea*, which extends for several kilometers inland from this riverside locality (Wiley, 2010). According to Valqui (2001)—most of whose voucher specimens (at the UF) were correctly identified—this species was found to be "restricted to streambeds of small to medium size streams of primary terra firme forest, where they are often the most abundant spiny rat." The lack of consistency in these data suggest that *P. cuvieri* is a habitat generalist, at least in our region.

Proechimys kulinae da Silva, 1998

Figures 56C, 56F

VOUCHER MATERIAL (*N* = 119): Jenaro Herrera (AMNH 276707, 276708; MUSM 23826, 23828, 23832), Nuevo San Juan (AMNH 272705, 272714; MUSM 11300, 13340, 13348), San Pedro (MVZ 198489; UF 30551, 30573, 30578, 30579, 30582, 30583, 30586, 30588, 30592–30595, 30597, 30598, 30600, 30601, 30606, 30607, 30611–30614, 30616–30618, 30621–30624, 30627, 30630–30636, 30638, 30640–30646, 30648–30650, 30652, 30653, 30655, 30662–30690, 30692–30697, 30699, 30701–30709, 30711, 30712, 30714–30719, 30765, 30766), Santa Cecilia (FMNH 87240), Siete de Julio (UF 30710). Additionally, Medina et al. (2015) reported specimens from Quebrada Sábalo that we have not examined.

UNVOUCHERED OBSERVATIONS: Field identifications of this species cannot be accepted as valid without supporting voucher material.

IDENTIFICATION: *Proechimys kulinae* is a distinctively small species of spiny rat that does not overlap (or only minimally overlaps) other local species in several external and craniodental dimensions, notably including length of the hind foot and length of the maxillary toothrow (table 40). The dorsal pelage is unremarkably brownish, and the ventral pelage is abruptly white from chin to anus. The ventral fur is thin and feels harsh to the touch because it consists mostly of soft spines with only a few wool hairs mixed among them.

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[42] The mean value for CIL in the Juruá series according to Patton et al.'s (2000) table 64 is 39.6 mm, which is the same value as the sample minimum provided in the next column. Most of the Juruá series has been returned to Brazil, but the mean value for CIL computed from measurements of 10 specimens remaining at the MVZ is 45.6 mm (J.L. Patton, personal commun.), which is very close to the corresponding mean in our series.

The hind foot is mostly covered with whitish hairs, but in some specimens (e.g., AMNH 276707, MUSM 23826) it is bicolored, with abruptly darker hairs over the lateral metatarsals. The nine bacula we examined resemble the morphology illustrated by da Silva et al. (1998: fig. 6): they are moderately long (7.7 mm on average), slender (2.3 mm in basal width), and lack well-developed distal processes, although our specimens have a somewhat larger basal-width-to-length ratio (mean = 0.30, range = 0.26–0.37) than the six examples they measured.

Distinctive craniodental features of *Proechimys kulinae* include parallel-sided, ovate, or weakly lyrate incisive foramina that have complete septa in most of the specimens we examined. The premaxillary portion of the incisive septum is usually short, and the maxillary portion is usually weakly keeled (never strongly keeled as in *P. brevicauda*); the vomer is usually concealed, but it is exposed in a few specimens. The anterior palate lacks strong relief in some specimens (e.g., AMNH 272707, 272714), but it is distinctly grooved-and-ridged in others (MUSM 11300, MVZ 198489). The floor of the infraorbital foramen is smooth, apparently never with a well-developed canal for the infraorbital nerve. The mesopterygoid fossa penetrates deeply between the third molars and sometimes extends to or between the second molars (mean score for mesopterygoid penetration = 3.5, range = 3–4). A distinctive cranial trait is the usual presence of a long extension of the temporal crest onto the parietal. There are never more than three labial folds on any upper cheektooth, but M3 occasionally has only two labial folds, so the sample formula for our material is 3-3-3-3(2).

Our specimens closely resemble the original description of *Proechimys kulinae* provided by da Silva (1998), and measurements of our specimens broadly overlap those of her type series from the Rio Juruá. The results of phylogenetic analyses of DNA sequence data obtained from two of our specimens (AMNH 272714, MUSM 123828) are likewise consistent with our specimen identifications (Dalapicolla, 2024: appendix E, fig. S5).

ETHNOBIOLOGY: The Matses have no special name for this species.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: Six specimens of *Proechimys kulinae* are accompanied by habitat data from our region. Of these, two were taken in primary upland forest near Nuevo San Juan, and four were taken in primary white-sand forest near Jenaro Herrera; all were trapped on the ground. According to Valqui (2001)—most of whose voucher specimens (at the UF) were correctly identified—this species "occurs exclusively in primary terra firme forests, where it is the most abundant species."

Proechimys quadruplicatus Hershkovitz, 1948

Figures 57A, 57D

VOUCHER MATERIAL (N = 51): El Chino (MVZ 198518, 198534; UF 30720–30735, 30737–30752), Orosa (AMNH 73801–73814), San Pedro (UF 30615, 30657, 30736).

UNVOUCHERED OBSERVATIONS: Field identifications of this species cannot be accepted as valid without supporting voucher material.

IDENTIFICATION: *Proechimys quadruplicatus* is a large species that, in our region, has unremarkably brownish dorsal pelage—near Ridgway's (1912) Dresden Brown or Snuff Brown—and abruptly pure-white ventral pelage. The ventral fur is somewhat denser and softer than those of most (but not all) other species in the region. The hind feet are distinctly bicolored in most specimens, with whitish hairs over the medial metatarsals and brownish hairs over the lateral aspect of the foot. The baculum is small in proportion to body size (9.2 mm in length and 3.3 mm in proximal width, on average, in three fully mature specimens), with weakly developed apical processes and an average width-to-length ratio of 0.35 (range = 0.33–0.37).

The incisive foramina are lyrate, weakly so in most examined specimens, but sometimes strongly; one specimen (AMNH 73807), how-
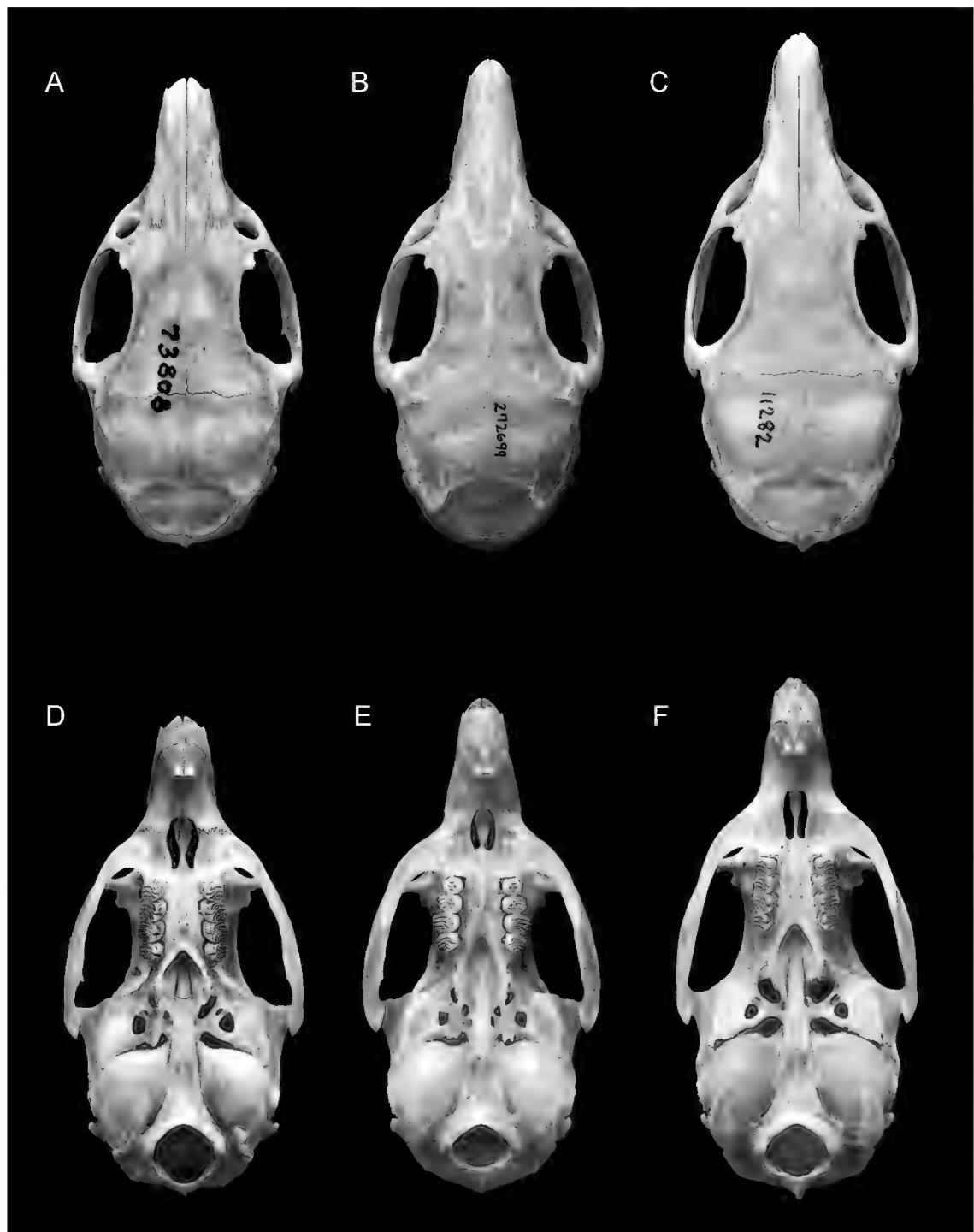
FIG. 57. Dorsal and ventral cranial views of *Proechimys quadruplicatus* (**A**, **D**; AMNH 73808), *P. simonsi* (**B**, **E**; AMNH 272699), and *P. steerei* (**C**, **F**; MUSM 11282). All views about ×1.4.

ever, has more or less oval foramina, and another (UF 30750) has foramina with subparallel margins. The incisive septum is complete in only about half the specimens we examined. The premaxillary part of the septum is usually short, and the vomerine portion is usually concealed, whereas the maxillary process is usually long, slender, and strongly keeled. The anterior palate is grooved in most specimens (strongly grooved in some), but it is more or less smooth in others (e.g., AMNH 73808). The mesopterygoid fossa always penetrates at least between the third molars and often between the second molars, resulting in an average mesopterygoid penetration score of 2.8 (range = 2–4). The floor of the infraorbital foramen often has a distinct groove for the infraorbital nerve, but it is occasionally quite smooth (e.g., in AMNH 73813). The temporal crest usually extends onto the parietals, sometimes for only a short distance, but often to a point just above the postglenoid foramen. Almost all lightly worn upper cheekteeth have four labial folds, although the posteriormost fold is often lost with advancing toothwear; the sample formula for our sample (based on minimally worn teeth) appears to be 4-4-4(3)-4(3). Craniodental measurements of our specimens (table 41) broadly overlap those of Hershkovitz's (1948) type series from eastern Ecuador.

The specimens from Orosa were identified by Patton and Leite (2015) as *Proechimys steerei*, but they are morphologically indistinguishable from the El Chino specimens that those authors referred to *P. quadruplicatus*. Although El Chino is south of the Amazon, Patton and Leite (2015: map 522) plotted this locality on the north bank of the river, an obvious lapsus. *Proechimys quadruplicatus* and *P. steerei*—both members of the Goeldii Group—are morphologically similar, but the mtDNA clades that we associate with these names (fig. 54, table 38) are vouchered by specimens that differ in external and dental characteristics. Whereas specimens of *P. quadruplicatus* (e.g., those from El Chino and Orosa) have drab-brownish dorsal fur, the specimens we identify as *P. steerei* (from Nuevo San Juan) have brighter,

reddish-brown dorsal fur. Additionally, the predominance of 4-4-4-4 labial folds in the upper cheekteeth of both the El Chino and Orosa series (*P. quadruplicatus*) contrasts with our observation of 3-3-4-3 folds in the series from Nuevo San Juan (*P. steerei*). The diagnostic value of frequency differences that we observed in several other characters (table 39) are hard to interpret as taxonomic evidence due to the small size of our *P. steerei* sample (comprising only four adults; see below).

ETHNOBIOLOGY: The Matses have no special name for this species.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: None of the specimens of *Proechimys quadruplicatus* from our region are accompanied by habitat information, but the series from Orosa was probably collected in *várzea*, which extends inland for several kilometers at this riverside locality (Wiley, 2010). According to Valqui (2001)—most of whose voucher specimens (at the UF) were correctly identified—this species is "a strict *várzea* specialist ... it is the only spiny rat species in true seasonally flooded forest, especially in areas far from terra firme habitats."

Proechimys simonsi Thomas, 1900

Figures 57B, 57E

VOUCHER MATERIAL (*N* = 54): Jenaro Herrera (MUSM 23829), Nuevo San Juan (AMNH 268277, 268278, 268280, 272670, 272677, 272690, 272693, 272699, 272716, 272717, 272720; MUSM 11260, 11276, 11294, 11299, 11314, 13339, 13341–13345, 13349, 13350), Orosa (AMNH 74093, 74094), San Pedro (UF 30580, 30596, 30602, 30605, 30698, 30753–30764, 30770–30773, 30786), Siete de Julio (UF 30767, 30768, 30776, 30779, 30781). Pavlinov (1994) reported additional specimens from Jenaro Herrera (at the ZMMU) that we have not seen.

UNVOUCHERED OBSERVATIONS: Field identifications of this species cannot be accepted as valid without supporting voucher material.

TABLE 41

External and Craniodental Measurements (mm) and Weights (g) of *Proechimys quadruplicatus*, *P. simonsi*, and *P. steerei* from the Yavarí-Ucayali Interfluvial Region

	P. quadruplicatus[a]	P. simonsi[b]	P. steerei[c]
HBL	230 ± 10 (220–241) 6	223 ± 20 (190–257) 18	255 ± 15 (236–271) 4
LT	140 ± 11 (125–155) 6	178 ± 16 (150–210) 16	172 ± 8 (164–179) 3
HF	52 ± 3 (46–57) 16	48 ± 3 (43–53) 19	55 ± 2 (52–57) 4
Ear	20 ± 0 (20–21) 6	23 ± 1 (21–26) 19	23 ± 2 (21–25) 4
CIL	47.4 ± 2.2 (44.0–51.7) 12	44.4 ± 2.4 (41.1–50.2) 18	51.7 ± 2.4 (48.7–53.7) 4
LD	12.2 ± 0.6 (11.0–13.1) 17	11.3 ± 0.8 (10.2–13.1) 21	12.8 ± 0.6 (12.0–13.5) 4
MTR	8.9 ± 0.4 (8.3–9.6) 17	8.4 ± 0.4 (7.7–9.3) 21	8.8 ± 0.6 (8.4–9.6) 4
LIF	5.6 ± 0.8 (4.2–6.7) 17	4.6 ± 0.4 (3.8–5.5) 21	6.3 ± 0.8 (5.3–7.2) 4
BIF	2.8 ± 0.3 (2.1–3.6) 17	2.6 ± 0.3 (1.9–3.2) 21	2.9 ± 0.2 (2.7–3.2) 4
LN	22.1 ± 2.0 (19.0–24.9) 17	21.4 ± 1.6 (19.0–24.5) 19	24.6 ± 1.3 (23.3–25.9) 4
LIB	12.6 ± 0.9 (11.4–14.8) 17	11.4 ± 0.4 (10.3–12.3) 21	12.4 ± 0.6 (11.9–13.2) 4
ZL	19.1 ± 1.0 (17.0–21.3) 17	17.1 ± 1.0 (15.4–19.3) 20	21.1 ± 1.3 (19.4–22.1) 4
ZB	27.5 ± 1.2 (25.8–29.6) 16	25.5 ± 1.3 (22.3–27.7) 20	28.0 ± 0.9 (27.2–29.1) 4
Weight	370 ± 38 (315–425) 7	297 ± 65 (190–405) 18	532 ± 56 (484–609) 4

[a] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 73801–73805, 73807, 73808, 73813, 73814; MVZ 198518, 198534; UF 30724, 30730, 30740, 30743, 30747, 30750.

[b] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: AMNH 74093, 268277, 268278, 272693, 272699, 272716, 272717; MUSM 11260, 11276, 11294, 11299, 11314, 13342–13344; MVZ 198498; UF 30754, 30761, 30762, 30767, 30772.

[c] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series: MUSM 11278, 11279, 11281, 11282.

IDENTIFICATION: *Proechimys simonsi* is a large species with unremarkably brownish dorsal fur and abruptly pure-white ventral fur that is unmarked by any darker pigment from chin to anus. As in most other congeners, the ventral fur is thin and feels harsh because it consists mostly of soft spines with only a few wool hairs mixed among them. The hind feet of most of the specimens we examined are indistinctly bicolored, with whitish hairs over the medial metatarsals and brownish hairs over the lateral aspect of the foot. The baculum is long and slender, lacks distinct apical processes, and averages 8.8 mm in length and 1.7 mm in proximal width (measurements from four specimens) with an average width-to-length ratio of 0.20 (range = 0.16–0.25).

The skull of this species has distinctively short incisive foramina (table 41) that are usually ovate but occasionally have subparallel lateral margins. The incisive septum is incomplete in 14 of 20 specimens (70%) that we scored for this trait, the premaxillary portion of the septum is usually short, and the vomer is almost always concealed; the maxillary portion of the septum sometimes has a weakly developed keel (e.g., in MUSM 13344), but seldom has more than a short median ridge. No grooves extend from the incisive foramina onto the anterior palate, which is smooth (ridge- and grooveless) in all the specimens we examined. The mesopterygoid fossa penetrates deeply between the toothrows, always at least between the anterior parts of the third molars but often also between the second molars

(average mesopterygoid penetration score = 3.4, range = 3–4). There is usually a distinct groove for the infraorbital nerve in the floor of the infraorbital foramen (mean score for this character = 1.8, range = 1–2). There are usually three labial folds on all the upper cheekteeth, but M2 and M3 occasionally have four folds each, so the sample formula is 3-3-3(4)-3(4).

Specimens of *Proechimys simonsi* from the Yavarí-Ucayali interfluve agree in most respects with Patton and Leite's (2015) description, with the following exceptions: (1) Skins of our specimens are unremarkably brownish rather than "reddish brown," a term that properly applies only to *P. steerei* in our material; and (2) this species is not unique in lacking a hypothenar pad on the hindfoot, because a hypothenar pad is also often absent in *P. kulinae* (see da Silva, 1998). Furthermore, a hypothenar pad is occasionally present on both the left and right hind feet of some of our specimens of *P. simonsi* (e.g., AMNH 272717), so this trait should be used cautiously (like any other) for taxonomic identifications.

DNA sequence data obtained from one of our voucher specimens (MUSM 13342) belong to the southern haplogroup of *Proechimys simonsi* (sensu Patton and Leite, 2015; see Dalapicolla et al., 2024: appendix E, fig. S6), which differs from an allegedly conspecific northern haplogroup by about 13% at the cytochrome *b* locus (J.L. Patton, personal commun.). The name *P. simonsi* (based on a type from Junín department) unambiguously applies to the southern haplogroup, whereas *P. nigrofulvus* Osgood, 1944 (based on a type from eastern Ecuador), is available for the northern haplogroup should future research indicate that it merits taxonomic separation.

ETHNOBIOLOGY: The Matses have no special name for this species.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: Fourteen specimens of *Proechimys simonsi* from our region are accompanied by habitat information. Of these, 13 were taken in upland primary forest, and one was taken in secondary vegetation. Most specimens were trapped on the ground, but one was taken in a trap tied to a liana about 1 m above the forest floor. According to Valqui (2001)—most of whose voucher specimens (at the UF) were correctly identified—this species "was captured in all habitats of terra firme."

Proechimys steerei Goldman, 1911

Figures 57C, 57F

VOUCHER MATERIAL (*N* = 5): Nuevo San Juan (AMNH 268279; MUSM 11278, 11279, 11281, 11282). Pacheco (1991) and Pavlinov (1994) also recorded this species from Jenaro Herrera based on material (at MUSM and ZMMU, respectively) that we have not seen.

UNVOUCHERED OBSERVATIONS: Field identifications of this species cannot be accepted as valid without supporting voucher material.

IDENTIFICATION: The four adult specimens we identify as *Proechimys steerei* are large rats with rich reddish-brown dorsal pelage—close to Ridgway's (1912) Amber Brown or Chestnut—and pure-white ventral fur that is noticeably denser and softer than the ventral fur of other sympatric congeners. The hind feet are mostly dark, but there is an indistinct streak of whitish hairs along the medial metatarsus that extends distally to the base of digit I. The tail is bicolored (dark above, paler below), but this marking is not as sharp as it is in other sympatric congeners (e.g., *P. simonsi*). The baculum (which we examined from two specimens) seems remarkably small for such big rats (only 8.4–9.6 mm long and 2.2–2.7 mm wide basally) and it has indistinct apical processes.

The incisive foramina are long and weakly lyrate with a complete septum composed of a short premaxillary process and a very long, narrow, and strongly keeled maxillary process; the vomer is concealed in three of our four adult specimens. Distinct grooves extend posteriorly from the incisive foramina onto the anterior palate, where they are separated by a low median ridge. The mesopterygoid fossa does not extend

between the toothrows in one specimen, penetrates only between the M3 hypocones in two others, and extends between the M3 protocones in the fourth. The floor of the infraorbital foramen is grooved by a rather weakly defined nerve canal, and the temporal crests usually extend only a short distance onto the parietals. Examined specimens have either 3-3-4-3 or 3-3-3-3 labial folds on the upper cheekteeth. In all these respects our material resembles the morphology of *P. steerei* as described by Patton and Leite (2015), and measurements of our series (table 41) fall within the range of variation reported by Patton et al. (2000: table 78) for their Rio Juruá material.

ETHNOBIOLOGY: The Matses have no special name for this species.

MATSES NATURAL HISTORY: No interviews were focused on this species.

REMARKS: Our four adult specimens were trapped on the ground in the floodplain of the Río Gálvez—one in seasonally flooded forest and three in primary forest on a levee island surrounded by seasonally flooded forest. One juvenile was trapped near the river, but in secondary upland forest.

DISCUSSION

Rodent Faunal Composition and Biogeography

This report documents the occurrence of 40 species of rodents in the Yavarí-Ucayali interfluve, a total that is based on 740 examined specimens and numerous unvouchered observations from 28 localities scattered throughout our region (fig. 2, table 42). The cumulative faunal-sampling effort that produced these specimens and occurrence data included ca. 64,000 trap-nights at ground level using standard equipment (commercially manufactured snap traps and live traps), mostly at San Pedro and Nuevo San Juan; 2150 trap-nights of arboreal trapping and 2750 bucket-nights of pitfall trapping at Jenaro Herrera; 409 hours of nocturnal hunting at Nuevo San Juan; and almost 3000 km of nocturnal and diurnal visual-tran-

sect census at another 10 localities (Voss and Fleck, 2017; Voss et al., 2019). Our fieldwork at Nuevo San Juan from 1995 to 1999 was additionally supplemented by unquantified but frequent trapping and haphazard captures by Matses collaborators.

Nevertheless, it is possible that our rodent inventory is incomplete. Unfortunately, we lack appropriate frequency data to statistically estimate inventory completeness, although it is relevant to note that all the species known to occur in our region have been recorded multiple times.[43] At least four additional species could be expected to occur locally based on geographic range data (appendix 5): each is known from localities north and south of the Yavarí-Ucayali interfluve, and two of them (*Daptomys peruviensis* and *Rhipidomys leucodactylus*) are notoriously elusive. If all four species really do occur in our region, then the total rodent fauna includes 44 species, and our inventory is about 90% complete.

Fewer species than the regional total are known to occur at each of the three sites most intensively surveyed for rodents in our region—Jenaro Herrera, Nuevo San Juan, and San Pedro (table 42)—but methodological omissions suggest that none of these places was exhaustively sampled. Of the four methods deemed essential for obtaining complete inventories of nonvolant mammalian faunas in Neotropical rainforests (Voss and Emmons, 1996), intensive terrestrial trapping was only carried out at Nuevo San Juan and San Pedro, arboreal trapping and pitfall trapping was only carried out at Jenaro Herrera, and nocturnal hunting was only done at Nuevo San Juan (table 43). Without additional, methodologically complementary fieldwork at these sites, it is hard to know how many species in the regional fauna can occur sympatrically. However, the Yavarí-Ucayali interfluve is not transected by known biogeographic barriers, so

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[43] The heuristic "stop rules" proposed by Colwell and Coddington (1994) suggest that an inventory is complete when all species have been observed at least twice.

TABLE 42

Rodent Species Identified from Specimens or Observations In the Yavarí-Ucayali Interfluve

	Localities[a]				Specimens examined[b]
	NSJ	JH	SP	Other	
Sciurillus pusillus	X	(X)	(X)	X	10
Sciurus pachecoi	X		(X)	X	26
Sciurus pyrrhinus	X	X	(X)	X	22
Sciurus spadiceus	X	(X)	(X)	X	41
Sciurus flaviventer	X		(X)	X	28
Amphinectomys savamis		X	X	(X)	2
Euryoryzomys macconnelli	X	X	X	(X)	35
Holochilus nanus		(X)		X	13
Hylaeamys perenensis	X	(X)	X	X	33
Hylaeamys yunganus	X	(X)	X	X	12
Neacomys aletheia	X	X		(X)	17
Neacomys musseri	X				6
Nectomys apicalis	X		X		12
Nectomys rattus		X		X	6
Oecomys bicolor	X	X	X	X	22
Oecomys nanus		X			12
Oecomys makampi	X				2
Oecomys galvez	X	X			11
Oecomys roberti	X	X			7
Oligoryzomys microtis		(X)	X	X	15
Scolomys melanops	X	X		(X)	3
Scolomys ucayalensis	X	X	(X)	(X)	16
Hydrochoerus hydrochaeris	X	(X)	(X)	X	2
Cuniculus paca	X	(X)	(X)	X	3
Dasyprocta fuliginosa	X	(X)	(X)	X	8
Myoprocta pratti	X	X	(X)	X	20
Dinomys branickii	X			(X)	1
Coendou ichillus				(X)	0
Coendou longicaudatus	X	(X)	(X)	X	6
Dactylomys dactylinus		(X)	(X)	X	16
Isothrix bistriata	X		(X)	X	16
Makalata "species 5"	X				4
Mesomys hispidus	X		X	X	9
Toromys rhipidurus		X	X	X	10
Proechimys brevicauda	X	(X)	X	X	27
Proechimys cuvieri	X		X	X	38
Proechimys kulinae	X	X	X	X	119
Proechimys quadruplicatus			X	X	51
Proechimys simonsi	X	X	X	X	54
Proechimys steerei	X	(X)			5
Total sympatric species:	31	28	27	—	

[a] Abbreviations: NSJ, Nuevo San Juan; JH, Jenaro Herrera; SP, San Pedro. Column entries: X = known from examined specimens, (X) = unvouchered sighting, photographs, or unexamined specimens.
[b] Specimens examined for this report from the Yavarí-Ucayali interfluve.

TABLE 43

Faunal-sampling Effort at Three Inventory Sites in the Yavarí-Ucayali Interfluve

Methods[a]	Jenaro Herrera	Nuevo San Juan	San Pedro
Terrestrial trapping	unknown	>12,286 trap-nights[b]	51,700 trap-nights[c]
Arboreal trapping	2150 trap-nights	—	—
Pitfall trapping	2750 bucket-nights	—	—
Nocturnal hunting	—	409 hours	—

[a] As described by Voss and Emmons (1996).
[b] Trapping by Matses children and adults with borrowed live traps and deadfalls from 1995 to 1999 was not quantified.
[c] Valqui (2001).

sympatric species richness in our region is probably constrained only by habitat occupancy.

Faunally significant site-to-site habitat differences in the Yavarí-Ucayali interfluve consist primarily of the presence of seasonally flooded forests along major rivers and the absence of such forests at upland sites. Based on data summarized or cited in this report, it seems likely that several rodent species (e.g., *Amphinectomys savamis, Oecomys roberti, Dactylomys dactylinus, Isothrix bistriata, Makalata* "species 5," *Toromys rhipidurus, Proechimys quadruplicatus*, and *P. steerei*) are associated with seasonally flooded forest, but another three species (*Holochilus nanus, Oligoryzomys microtis*, and *Hydrochoerus hydrochaeris*) occur along river margins. These 11 riparian taxa are unlikely to occur at upland sites, which might, therefore, support no more than about 30 sympatric rodents in our region.[44] By contrast, sites with both upland (terra firme) forest and flooded forests could have more sympatric (but not syntopic) species. Flooded forest occurs along the Río Gálvez at Nuevo San Juan, along the Quebrada Blanco at San Pedro, and along the Ucayali near Jenaro Herrera, but most faunal sampling at all three sites was confined to terra firme habitats. In effect, it would be reasonable to expect that 30–40 rodent species might be sympatric throughout the Yavarí-Ucayali inter-

fluve, unless the remote white-sand forests of the Río Blanco (Pitman et al., 2015)—as yet unsurveyed for small nonvolant mammals—have more depauperate faunas.

The higher-taxonomic composition of the Yavarí-Ucayali interfluvial rodent fauna is, with one exception, typical of rodent faunas found throughout Amazonia, where the families Sciuridae, Cricetidae, Caviidae, Dasyproctidae, Cuniculidae, Erethizontidae, and Echimyidae are ubiquitous (Voss and Emmons, 1996). The exception, Dinomyidae, is restricted to westernmost Amazonia, usually within a few hundred kilometers of the Andes. Most of the rodent genera that occur in our region are likewise widely distributed, although two (*Amphinectomys* and *Scolomys*) are western Amazonian endemics. Instead, the distinctive attributes of our regional rodent fauna concern its species composition.

First, the Yavarí-Ucayali interfluvial rodent fauna is remarkably speciose. By comparison with the thoroughly inventoried fauna of northern French Guiana, for example, our region has about 40% more observed species and about 50% more expected species (fig. 58, table 44). As documented elsewhere (Voss, MS), this regional disparity in species numbers is also seen in primates (of which 14 species are known from the Yavarí-Ucayali interfluve versus six species in northern French Guiana) and to a lesser extent also in didelphimorphians (19 species in the Yavarí-Ucayali interfluve versus 15 species in northern French Guiana). The explanation for such differences is perhaps to be

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[44] For the purpose of this discussion, upland sites are remote from open water, although they may be drained by shallow, first-order streams too small to create canopy gaps or to create seasonally flooded habitats.
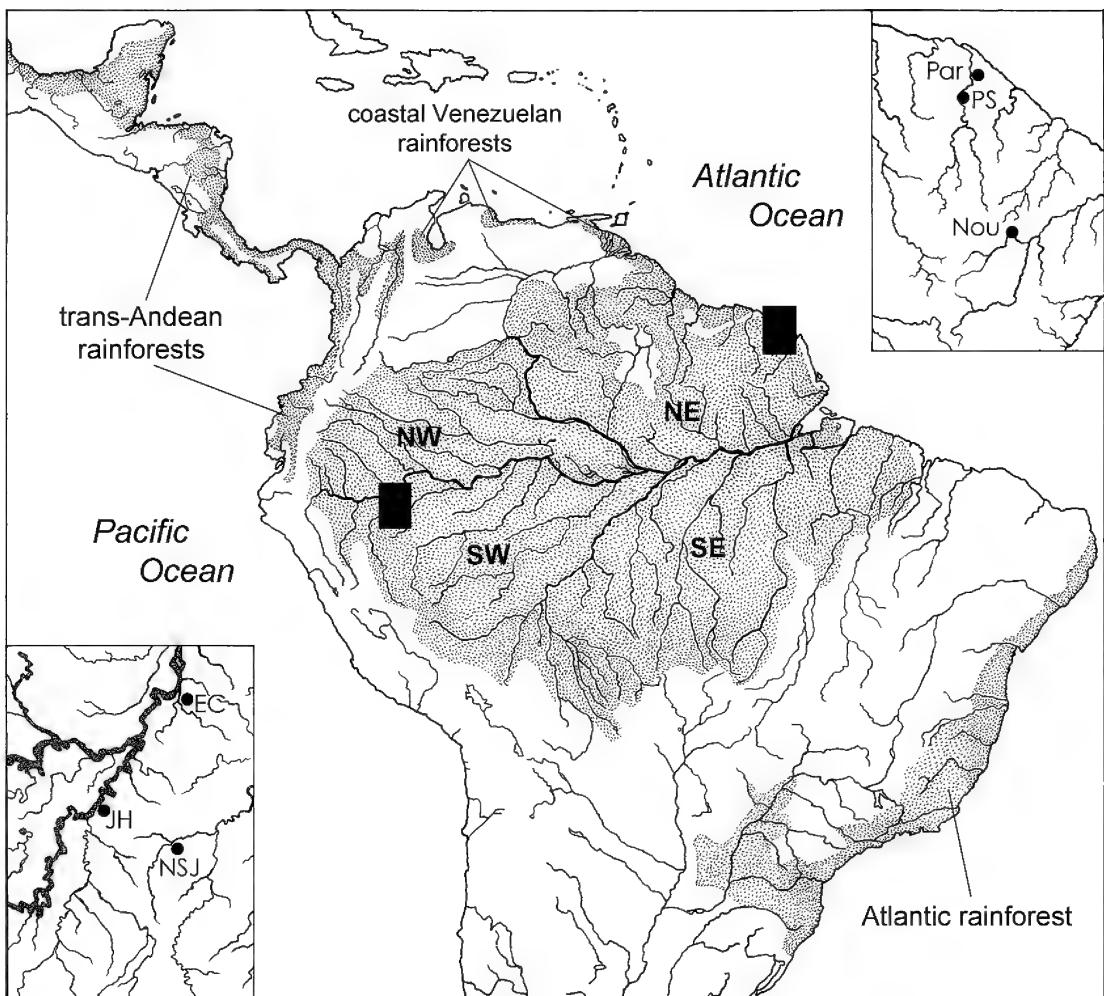
FIG. 58. Four Neotropical rainforest biomes (stippled) separated by montane or nonforest vegetation. Primary intercardinal directions (NE, NW, SE, SW) label quadrants of Amazonia defined by the Amazon, Negro, and Madeira rivers (after Wallace, 1854). Insets show the location of faunal inventory sites that include the entire known rodent faunas from the Yavarí-Ucayali interfluve (in SW Amazonia: **EC**, El Chino; **JH**, Jenaro Herrera; **NSJ**, Nuevo San Juan) and northern French Guiana (in NE Amazonia: **Par**, Paracou; **PS**, Petit Saut; **Nou**, Nouragues).

found in edaphic factors that result in higher primary productivity of western Amazonian by comparison with eastern Amazonian landscapes (Voss and Emmons, 1996), but a discussion of the supporting evidence is beyond the scope of this report. Numerical comparisons aside, however, the rodent fauna of the Yavarí-Ucayali interfluve is also biogeographically distinctive.

The species found in our region can be sorted into several groups based on their distributions among Amazonian quadrants defined by the Amazon River, the Rio Negro, and the Rio Madeira (fig. 58, table 45). Thirteen species—about one-third of the known fauna—are currently thought to be pan-Amazonian, but this biogeographically uninformative fraction will probably be reduced by

TABLE 44

Composition of Rainforest Rodent Faunas in the Yavarí-Ucayali Interfluve and Northern French Guiana

	Yavarí-Ucayali Interfluve[a]		Northern French Guiana[b]	
	Observed	Expected	Observed	Expected
Sciuridae	5	5	2	2
Cricetidae	17	21	14	15
Caviidae	1	1	1	1
Cuniculiudae	1	1	1	1
Dasyproctidae	2	2	2	2
Dinomyidae	1	1	0	0
Erethizontidae	2	2	2	2
Echimyidae	11	11	6	6
TOTALS	40	44	28	29

[a] As summarized in this report, but note that all the rodent species found in our region are known to occur in the combined species lists from just three sites: El Chino, Jenaro Herrera, and Nuevo San Juan.

[b] See figure 58. Observed species include those reported from Paracou (Voss et al., 2001), Petit Saut (Vié, 1999) and Nouragues (Feer and Charles-Dominique, 2001). The Nouragues list, however, includes two misidentifications (Voss et al., 2001): *Neacomys* "*guianae*" (= *N. dubosti* and/or *N. paracou*) and *Proechimys* "*cayennensis*" (= *P. guyannensis*). The only species missing from these inventories (expected but not observed) is *Holochilus nanus*.

ongoing revisionary research given the substantial sequence divergence known to exist among allegedly conspecific populations of *Sciurillus pusillus, Euryoryzomys macconnelli, Oecomys roberti, Mesomys hispidus,* and *Proechimys cuvieri*. Three other species are somewhat less widespread (occurring in three Amazonian quadrants: *Sciurus spadiceus, Nectomys rattus,* and *Oligoryzomys microtis*), but their distributions suggest no consistent biogeographic signal. By contrast, 23 species—over half the regional fauna—are known only from western Amazonia. Of these, 16 species (as currently understood) occur north and south of the upper Amazon, whereas seven species are southwestern Amazonian endemics.

Western Amazonian species that occur on both banks of the upper Amazon include two squirrels (*Sciurus pyrrhinus, S. flaviventer*), six cricetids (*Amphinectomys savamis, Hylaeamys perenensis, Nectomys apicalis, Oecomys galvez, Scolomys melanops, S. ucayalensis*), one dasyproctid (*Myoprocta pratti*), one dinomyid (*Dinomys branickii*), one erethizontid (*Coen-dou ichillus*), and five echimyids (*Isothrix bistriata, Toromys rhipidurus, Proechimys brevicauda, P. simonsi, P. steerei*). The upper Amazon is thought to be a significant dispersal barrier, so these species seem like biogeographic anomalies, but mtDNA sequence data suggest that several of them include reciprocally monophyletic haplogroups on opposite sides of the river (table 46). Future research is needed to determine whether such left- and right-bank clades merit taxonomic recognition.

The seven southwestern Amazonian (Inambari) endemics[45] include one squirrel (*Sciurus pachecoi*), four cricetids (*Neacomys aletheia, N. musseri, Oecomys makampi, O. nanus*), and two echimyids (*Makalata* "species 5," *Proechimys kulinae*). Although other rodents are endemic to southwestern Amazonia (e.g., *Neacomys minutus, Rhipidomys gardneri, Mesomys occultus, Toromys albiventris, Proechimys gardneri, P. pattoni;* see Patton et

[45] Wallace's (1854) notion of southwestern Amazonia is geographically equivalent to Cracraft's (1985) definition of the Inambari center of endemism.

TABLE 45

Biogeographic Classification of Rodents from the Yavarí-Ucayali Interfluve

Distribution[a]	Species
Pan-Amazonian (all four quadrants)	13
NE, NW, & SW	1
NE, SE, & SW	1
NW, SE, & SW	2
NW & SW	16
SW only	7
TOTAL	40

[a] Occurrence in Amazonian quadrants defined by the Amazon, Negro, and Madeira rivers (fig. 58; appendix 6).

al., 2015), they are not known to occur in the Yavarí-Ucayali interfluve. In fact, no rodent species endemic to southwestern Amazonia seems to occur throughout the immense wedge of land between the Rio Madeira and the upper Amazon, but the environmental factors or geographic barriers that limit their distributions is unknown. At least for rodents, the lack of compelling evidence for a southwestern Amazonian center of endemism based on codistributed species is noteworthy. Instead, southwestern Amazonia may consist either of several centers of rodent endemism, or site-to-site faunal turnover within this quadrant may reflect range limits of species that are independently affected by edaphic, rainfall, or other ecological gradients.

Matses Rodent Names and Knowledge of Rodent Natural History

Matses knowledge about rodents and their names for rodents (table 47) are consistent with the ethnobiological pattern described by Fleck and Voss (2006) and exemplified in earlier monographs of this series (e.g., Voss and Fleck, 2011, 2017). The Matses have much to say about the natural history of primary game species (species routinely hunted for food); less about secondary game species or nongame species with high salience; and little or nothing about small, inconspicuous, inedible, and morphologically indistinguishable taxa. Only two rodents—*Cuniculus paca* and *Dasyprocta agouti*—belong to the first category; the Matses hunt both species frequently and are well informed about their behavior and diets; each is uniquely known by a primary term (tambis and mekueste, respectively), but also by multiple synonyms or hyponyms (knowledge of which traditionally functioned in ritualized public displays of hunting expertise; Fleck and Voss, 2006). Rodent species in the second category include *Myoprocta pratti* (a secondary game species), all five species of squirrels (seldom if ever eaten but diurnal and highly visible), *Oecomys bicolor* (a household pest), *Hydrochoerus hydrochaeris* and *Coendou longicaudata* (large and morphologically unmistakable), *Isothrix bistriata* (visible by day and uniquely marked), and *Nectomys apicalis* and *Dinomys branickii* (both garden pests); each of these species has a unique name but only *M. pratti* has a synonym. Species in the third category include most cricetids and echimyids, which are known by collective terms (e.g., takbid umu) but lack unique identifiers. Although *Proechimys* has high cultural salience (both as garden pests and as tasty snack food), the five species known to occur in Matses territory do not have unique names, doubtless because they are morphologically difficult to distinguish.

Curiously, the Matses have no collective term corresponding to Rodentia, which is not even a covert category (Berlin et al., 1968) in their ethnozoological lexicon. This omission is not unusual, however, because the Matses also lack collective terms for other mammalian clades, including Primates, Xenarthra, Carnivora, and Artiodactyla. A plausible explanation is that the Matses seldom (if ever) need to refer collectively to rodents, monkeys, xenarthrans, carnivorans, or hooved mammals, so no sociocultural purpose is served by naming such abstract entities.

TABLE 46

**MtDNA Evidence for Reciprocal Monophyly of Western Amazonian Rodent Populations
North and South of the Amazon**

	Number of sequences		Reciprocally monophyletic?	Reference
	N bank	S bank		
Sciurus pyrrhinus	4	8	no	Abreu et al. (2020a)
Sciurus flaviventer	11	11	yes	Abreu et al. (2020a)
Hylaeamys perenensis	1	14	no	Patton et al. (2000)
Nectomys apicalis	9	7	no	M. Weksler[a]
Oecomys galvez	6	7	yes	this report
Isothrix bistriata	1	10	no	Patton et al. (2000)
Proechimys brevicauda	3	7	no	Patton et al. (2000)
Proechimys simonsi	1	19	yes	Patton et al. (2000)
Proechimys steerei	5	17	yes	Patton et al. (2000)

[a] Personal commun. (18 May 2022).

As assessed by our comparisons with the scientific literature, most Matses natural history observations about rodents seem reasonably accurate—at least insofar as they correspond to published research results—or plausibly complement existing scientific sources (e.g., by listing previously unrecorded palm species with seeds consumed by giant squirrels). In other cases, Matses observations suggest potentially interesting differences between the behaviors of western Amazonian species and those of allopatric congeners previously studied by researchers; for example, the Matses assertion that *Dasyprocta fuliginosa* is solitary, whereas *D. leporina* (from northeastern Amazonia) is reported to live as monogamous pairs. In yet other cases, Matses observations suggest previously unsuspected habits of widespread species (e.g., snail eating by *Cuniculus paca*) that merit the attention of future field research. Lastly, we note occasional discrepancies with the scientific literature that seem likely to reflect erroneous observations or unjustified assumptions by Matses informants (e.g., their suggestion that *Microsciurus flaviventer* consumes the endosperm of extremely hard palm nuts). Overall, as previously assessed in other reports of this series,

Matses observations about routinely hunted and/or culturally salient species seem highly credible, even when they are not corroborated by published research results, whereas their observations about less frequently encountered species should be treated with some caution, especially when they conflict with the scientific literature.

Summary Comments on Mammals of the Yavarí-Ucayali Interfluve

This monograph concludes our series on the mammalian fauna of the Yavarí-Ucayali interfluve, which has been visited by commercial collectors and scientific researchers for almost a century. As detailed in this report and others that preceded it (Voss and Fleck, 2011, 2017; Voss et al., 2019; Velazco et al., 2021), thousands of collected specimens were examined and hundreds of unvouchered observations were evaluated from dozens of sites scattered throughout the region. Additionally, our Matses collaborators shared their knowledge of the local fauna gleaned from multiple lifetimes of hunting experience in the forest surrounding Nuevo San Juan and other settlements along the Río Gálvez and the Quebrada Chobayacu.

TABLE 47

Matses Folk Taxonomy for Rodents

Matses name[a]	Referent
kapa	general term for squirrels
kapa piu "red squirrel"	*Sciurus pyrrhinus* & *S. spadiceus* (red phase)
kapa ҫhëşhë "black squirrel"	*Sciurus spadiceus* (black phase)
kapampi "little squirrel"	*Sciurus pachecoi*
kapa kudu "gray squirrel"	*Sciurus flaviventer*
kaksi	*Sciurillus pusillus*
tambisëmpi "little paca"	general term for mice and rats
maka tanun "gray rat"	*Nectomys apicalis*
takbid umu "gray belly"	*Euryoryzomys macconnelli*, *Hylaeamys* spp., & *Scolomys* spp.
abuk makampi "little up rat"	*Oecomys* spp.
şhubu pekid "thatch eater"	*Oecomys bicolor*
şhëa	unidentified mouse
abuk maka "up rat"	general term for tree rats
abuk maka dëtan "striped-nose up rat"	*Isothrix bistriata*
abuk maka kapinchuk chokid "spiny-back up rat"	*Makalata* "sp. 5" & *Mesomys hispidus*
tambisëmpi "little paca"	*Proechimys* spp.
isa	*Coendou longicaudatus*
tambisbiekkid "one similar to a paca"	*Dinomys branickii*
mëkueste	*Dasyprocta fuliginosa*
tsikudu (synonym) "gray rump"	
mëkuestedapa (variety) "big agouti"	
mentsod (variety)	
tsatsin	*Myoprocta pratti*
ҫhoҫhoşh (onomatapoetic synonym)	
tambis	*Cuniculus paca*
made (synonym)	
mapua (synonym)	
tampodo (synonym)	
tambis ҫhëşhë (variety) "dark paca"	
tambis uşhu (variety) "light-colored paca"	
tambis piu (variety) "red paca"	

[a] Excluding regional variants (see text).

It is, obviously, difficult to quantify whole-faunal sampling effort from such disparate sources, but inventory completeness was assessed for subsets of the fauna using both nonparametric statistics and/or range maps (table 48). There can be no certainty in such inferences, but it would be reasonable to expect as many as 228 species of terrestrial mammals (excluding manatees and dolphins) in the Yavarí-Ucayali interfluve, of which about 92% (201 species) are definitely known to occur there.

As previously mentioned, the Yavarí-Ucayali interfluve lacks known internal dispersal

TABLE 48

Observed and Expected Nonaquatic Mammalian Species in the Yavarí-Ucayali Interfluve

	Species		Reference
	Observed	Expected	
Didelphimorphia	19	23	Voss et al. (2019)
Xenarthra	9	10	Voss & Fleck (2017)
Primates	14	14	Voss & Fleck (2011)
Chiroptera	98	116	Velazco et al. (2021)
Carnivora	16	16	Voss & Fleck (2017)
Perissodactyla	1	1	Voss & Fleck (2017)
Artiodactyla	4	4	Voss & Fleck (2017)
Rodentia	40	44	this report
TOTALS	201	228	

barriers for terrestrial vertebrates. All the streams that drain our region have headwaters in low hills (<200 m above sea level), and their lower reaches are meandering, with oxbow lakes that mark the episodic transfer of dry land from one bank to the other; none could effectively limit the movement of resident mammalian species across the interfluvial landscape for more than a few generations. On this assumption, sympatric species richness within our region is probably limited only by habitat availability.

In addition to the 11 riparian rodents discussed above, only five other mammals seem likely to be absent from upland sites in our region: *Rhynchonycteris naso*, *Saimiri sciureus*, *Lontra longicaudis*, *Pteronura brasiliensis*, and *Procyon cancrivorus*. Subtracting these 16 species from the totals in table 48 suggests that even sites far from major rivers in our region might have as few as 185 or as many as 212 sympatric species, but we really know nothing about source-sink dynamics (Pulliam, 1988) as they might affect mammalian populations in western Amazonian habitat mosaics. Many species that are known to occur in both terra firme and riparian forests might have their source populations in the latter habitat and be absent from extensive tracts of upland forest remote from major rivers. We currently have no idea whether or not this is true.

In effect, our monograph series provides only a first step toward understanding mammalian diversity in a large and still largely pristine tract of western Amazonian rainforest. Remarkably, the Yavarí-Ucayali interfluve is the only western Amazonian region for which a comprehensive taxonomic resource for mammalogical research is currently available. The region is close enough to a modern transportation hub (Iquitos) to be readily accessible to researchers, but that same proximity is a threat. Fast riverboat service now provides efficient transportation to and from markets in Iquitos, with the result that multiple villages along the lower Ucayali and the right (south) bank of the Amazon are growing rapidly, with unfortunate consequences. One of the best-sampled inventory sites in our region, Jenaro Herrera, is now largely defaunated by hunting and is no longer a suitable location for ecological fieldwork. More remote sites, however, such as the Estación Biológica Quebrada Blanco (Heymann et al., 2021) retain intact faunas and, with adequate capital investments, could provide essential infrastructure for urgently needed research on an exceptionally diverse mammalian fauna.

FIG. 59. Matses children with a spiny rat taken in a deadfall trap (Nuevo San Juan, 1996; photo by D.W.F.)

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APPENDIX 1

Gazetteer

Below we list the principal localities from which rodents were collected or observed in the Ucayali-Yavarí interfluvial region. Boldface identifies locality names as they appear in the text (alternative names or spellings are cited parenthetically). Except as noted, all localities are mapped in figure 2.

Actiamë (6°19′S, 73°09′W; Vriesendorp et al., 2006a): inventory site in the floodplain of the Río Yaquerana; surveyed for mammals by Jessica Amanzo from 2–7 November 2004 (Amanzo, 2006).

Amelia (formerly Nazareth; 4°20′N, 70°12′W): alleged collecting locality of Wilfred H. Osgood on left bank of lower Yavarí, but the only rodent specimen labelled by Osgood from this locality was not professionally prepared and may have been purchased from a local collector.

Anguila (6°16′S, 73°55′W; Pitman et al., 2015): inventory site in the headwaters of the Quebrada Yanayacu, a minor right-bank affluent of the Río Tapiche (q.v.); surveyed for mammals by Mario Escabedo-Torres from 14 to 20 October 2014 (Pitman et al., 2015).

Boca Río Yaquerana (ca. 5°12′S, 72°53′W): collecting locality of Celestino Kalinowski at the confluence of the Yaquerana with the Río Gálvez (q.v.) from 3–30 August 1957. The combined waters of the Yaquerana and the Gálvez form the Río Yavarí (Faura-Gaig, 1964), but the Yaquerana is sometimes also known as the Alto Yavarí (Faura-Gaig, 1964), not the "Alto Yaquerana" (contra Stephens and Traylor, 1983).

Bombo (ca. 7°19′S, 73°55′W; DMA, 1989) collecting locality of Harvey Bassler, who collected squirrels here on 25 January 1928. The Quebrada (or Río) Bombo is a right-bank tributary of the upper Río Tapiche (q.v.). Our coordinates correspond to the confluence of the two streams, which is only about 13 km SE of Jorge and Velazco's (2006) inventory site at Tapiche. It is not entirely clear, however, whether this historical locality is actually in our region (a settlement or rubber camp of this name might have been sited on the opposite bank of the Tapiche), nor whether every specimen so labelled was collected in the same place (Bassler's

labelling of mammals seems to have been careless on occasion).

Choncó (5°33′S, 73°36′W; Vriesendorp et al., 2006a): inventory site in hilly terrain between the Río Tapiche (q.v.) and the Río Gálvez (q.v.) surveyed for mammals by Jessica Amanzo from 25–28 October 2004 (Amanzo, 2006).

Divisor (7°12′S, 73°53′W; Vriesendorp et al., 2006b): inventory site near Tapiche (q.v.) east of the upper Río Tapiche (q.v.) in the Sierra del Divisor (250–600 m), surveyed for mammals by Maria Luisa Jorge and Paúl Velazco from 19 to 23 August 2005 (Jorge and Velazco, 2006).

El Chino (4°18′S, 73°14′W; Valqui, 2001): inventory site on lower Río Tahuayo, just downstream from confluence with the Quebrada Blanco (q.v.); surveyed for small mammals by Michael Valqui in July 1996 and August/September 1997. El Chino is on the right bank of the Tahuayo, but Valqui's (2001) collecting near El Chino was done on the less populated left bank of the river across from the village. "Marcial Tello's house" is one such sublocality on the left bank of the Tahuayo.

Estación Biológica Quebrada Blanco (4°21′S, 73°09′W; Heymann et al., 2021): research station near San Pedro (q.v.) on the Quebrada Blanco (q.v.) and adjacent to the Reserva Comunal Tamshiyacu-Tahuayo (q.v.).

Estirón (5°35′S, 73°01′W): Matses village on the lower Quebrada Chobayacu where D.W.F. resided for several years and made occasional observations of mammals.

Itia Tëbu (5°51′S, 73°46′W; Vriesendorp et al., 2006a): inventory site in white sand forest on the right bank of the Río Blanco (q.v.), surveyed for mammals by Jessica Amanzo from 29 October to 2 November 2004 (Amanzo, 2006).

Jenaro Herrera (sometimes misspelled "Genaro Herrera," "Genero Herrera," "Henaro Errera," or "Jenero Herrera"; 4°55′S, 73°40′W): botanical field station ca. 2.5 km inland from the right bank of the Río Ucayali surveyed for mammals by various research teams from 1978 to 2003 (Voss and Fleck, 2011: 10).

La Colmena (see San Pedro).

Marupa (ca. 3°28′S, 72°38′W; DMA, 1990): collecting locality on right (south) bank of Amazon just downstream from mouth of Río Napo. Hershkovitz (1977: 656, 928) erroneously placed this locality on the Río Marañón and claimed that the Olallas collected here, but Marupa lies well

below the confluence of the Marañón and the Ucayali, so it is unambiguously on the Amazon (Faura-Gaig, 1964). Furthermore, none of the Marupa skins we examined bear Olalla labels, nor are they prepared like Olalla-labelled skins from other localities. The Olallas' extensive correspondence with AMNH curators provides no evidence that they ever worked at this locality, and the dates associated with Marupa specimens (3–5 May 1926) are impossible to reconcile with the Olallas' known itineraries (Wiley, 2010).

Nazareth (see Amelia).

Nuevo San Juan (5°15′S, 73°10′W; IGN, 1995): Matses village on the right bank of the Río Gálvez, intensively sampled for mammals by D.W.F. from 1995 to 1999 and by R.S.V. from 19 May to 12 July 1998.

Orosa (ca. 3°32′S, 72°11′W; Wiley, 2010): collecting locality on the right (south) bank of the Amazon, where Alfonso and Ramón Olalla worked from 30 August to 11 December 1926 (probably near the modern village of San José de Orosa with above coordinates; Wiley, 2010). Hershkovitz (1977: 928) placed Orosa on the Río Marañón, but it is unambiguously on the Amazon (see Marupa).

Puerto Punga (ca. 6°14′S, 74°02′W; Stephens and Traylor, 1983): collecting locality on the Río Tapiche (q.v.) where Harvey Bassler collected squirrels on 7 November 1927. Our coordinates correspond to the mouth of the Río (or Quebrada) Punga, a right-bank tributary of the Tapiche.

Quebrada Betilia (headwater at 6°26′S, 73°24′W; Medina et al., 2015): tributary of the Río Blanco located in the northeastern section of the Zona Reservada Sierra del Divisor; surveyed for mammals in the wet season of 2013 by Medina et al. (2015).

Quebrada Blanco (also known as "Río Blanco"; mouth at ca. 4°19′S, 73°14′W; Valqui, 2001: fig. 2-2): right-bank tributary of the Río Tahuayo and site of faunal inventory fieldwork by Michael Valqui, some of which extended into the nearby Reserva Comunal Tamshiyacu-Tahuayo (q.v.). Valqui's (1999, 2001) inventory site at San Pedro (q.v.) was on the lower Quebrada Blanco. Not to be confused with the Río Blanco (q.v.), a tributary of the Río Tapiche.

Quebrada Chobayacu (not labelled in fig. 2): minor left-bank tributary of upper Río Yavarí (q.v.). The Matses village of Estirón (q.v.) is mapped on the lower Chobayacu.

Quebrada Esperanza (ca. 4°20′S, 71°55′S; Stephens and Traylor, 1983): collecting locality of Celestino Kalinowski on the left bank of the Río Yavarí-Mirím (q.v.) from 6–27 September 1957. Faura-Gaig (1964: 524) gave the coordinates of Quebrada Esperanza at its confluence with the Yavarí-Mirím as 4°18′S, 71°56′W.

Quebrada Lobo (headwater at 6°30′S, 73°37′W; Medina et al., 2015): tributary of the Río Blanco located in the northeastern section of the Zona Reservada Sierra del Divisor; surveyed for mammals in the wet season of 2013 by Medina et al. (2015).

Quebrada Pantaleón (headwater at 6°25′S, 73°32′W; Medina et al., 2015): tributary of the Río Blanco, located in the northeastern section of the Zona Reservada Sierra del Divisor; surveyed for mammals in the wet season of 2013 by Medina et al. (2015).

Quebrada Pobreza (5°59′S, 73°46′W; Pitman et al., 2015): inventory site on the eponymous stream, a left-bank affluent of the Río Blanco (q.v.), surveyed for mammals by Mario Escobedo-Torres from 20–26 October 2014 (Pitman et al., 2015).

Quebrada Sábalo (headwater at 6°22′S, 73°28′W; Medina et al., 2015): left-bank tributary of the Río Yaquerana located in the northeastern section of the Zona Reservada Sierra del Divisor; surveyed for mammals in the wet season of 2013 by Medina et al. (2015).

Quebrada Vainilla (ca. 3°32′S, 72°44′W; Robbins et al., 1991): collecting site on the eponymous stream, visited by LSUMZ ornithologists in 1983 (Robbins et al., 1991).

Reserva Comunal Tamshiyacu-Tahuayo (recently renamed the "Área de Conservación Regional-Comunal Tamshiyacu-Tahuayo"): a protected area of predominantly well-drained upland forest extending from the headwaters of the Río Tamshiyacu and the Río Tahuayo (both of which are right-bank tributaries of the Amazon) to the upper Río Yavarí-Mirím (a left-bank tributary of the Yavarí), comprising about 322,500 ha (Puertas and Bodmer, 1993: fig. 1).

Río Blanco (mouth at 5°34′S, 73°52′W; DMA, 1989): a right-bank tributary of the Río Tapiche (q.v.). Not to be confused with the Quebrada Blanco (sometimes also called the Río Blanco), a right-bank tributary of the Río Tahuayo (fig. 2, inset).

Río Gálvez (mouth at 5°12′S, 72°53′W; DMA, 1989): one of two principal headwater tributaries of the Río Yavarí (see Boca Río Yaquerana, above). Our inventory site at Nuevo San Juan (q.v.) was on the right bank of the middle Gálvez.

Río Manití (mouth at 3°27′S, 72°51′W; DMA, 1989): minor right-bank tributary of the Amazon downstream from Iquitos.

Río Orosa (mouth at 3°29′S, 72°03′W; Wiley, 2010): minor right-bank tributary of the Amazon, probably with mouth near Orosa (q.v.) in the early 1900s but now shifted downstream (Wiley, 2010: 40).

Río Tapiche (mouth at 5°03′S, 73°51′W; DMA, 1989): major right-bank tributary of the Ucayali upstream from Jenaro Herrera (q.v.). This river forms part of the western boundary of our region.

Río Yavarí (mouth at 4°21′S, 70°02′W; DMA, 1989): major right-bank tributary of the Amazon, formerly an important source of wild rubber but now almost uninhabited (Bodmer and Puertas, 2003).

Río Yavarí-Mirím (also known as the "Yavarí-Mirí," "Yavari-Mirín," or "Yavarí Chico"; mouth at 4°31′S, 71°44′W): principal left-bank tributary of the Río Yavarí.

San Fernando (4°09′S, 70°14′W; DMA, 1989): collecting locality of Celestino Kalinowski on left bank of lower Río Yavarí, 10–15 July 1957.

San Pedro (4°20′S, 73°12′W; Valqui, 2001): ribereño village on right bank of lower Quebrada Blanco (q.v.) adjacent to Reserva Comunal Tamshiyacu-Tahuayo (q.v.) and downstream from Estación Biológica Quebrada Blanco (q.v.). This was the primary site of faunal inventory fieldwork by Michael Valqui from 1993 to 1999, but his specimen labels and derivative database entries mention several sublocalities (within 5 km of the village) that include "La Colmena Camp," "Plateau in La Colmena," "agricultural fields E of village," "Huanaquiri's house," and "Quebrada Limón" (Valqui, 2001: figs. 2-2 and 2-3).

Santa Cecilia (3°33′S, 72°53′W; Robbins et al., 1991): collecting locality of Celestino Kalinowski on the right bank of the Río Manití (q.v.) from 27 December 1956 to 21 January 1957.

Siete de Julio (4°27′S, 73°03′W; Valqui, 2001): collecting locality of Michael Valqui 12 km upstream from San Pedro (q.v.) on the right bank of the Quebrada Blanco (q.v.). This locality is alternatively (or additionally) called "Venaduy" (in the MUSM database) or "Camp Venaduy" (in Valqui, 2001), and it is apparently the same site labelled as "7 de Junio" in Valqui's (2001: fig. 2-2) map.

Tapiche (7°12′S, 73°56′W; Vriesendorp et al., 2006b): inventory site on the right bank of the upper Río Tapiche (q.v.); surveyed for mammals by Maria Luisa Jorge and Paúl Velazco from 12–17 August 2005 (Jorge and Velazco, 2006).

Wiswincho (5°49′S, 73°52′W; Pitman et al., 2015): inventory site about 2 km from the left bank of the lower Río Blanco (q.v.); surveyed for mammals by Mario Escobedo-Torres from 9–14 October 2014 (Pitman et al., 2015).

Zarate (not located): collecting locality of Pekka Soini on Río Manití (q.v.) sometime in October 1970.

APPENDIX 2

Primers Used to Amplify Cytochrome *b*

Name[a]	Sequence	Reference
MVZ05	CGAAGCTTGATATGAAAAACCATCGTTG	Irwin et al., 1991
MVZ16	AAATAGGAARTATCAYTCTGGTTTRAT	Smith & Patton, 1993
Proechi-CYTB-20F	ACCACGACCAATGATATGAAAAACC	this study
Proechi-CYTB-342R	TATTGATGCTCCGTTGGCGT	this study
Proechi-CYTB-160F	GCATGATGAAACTTCGGCTC	this study
Proechi-CYTB-572R	CCTCAGATTCATTCTACGAGGGT	this study
Proechi-CYTB-323F	ACGCCAACGGAGCATCAATA	this study
Proechi-CYTB-741R	AGGGTGGAATGGGATTTTGTC	this study
Proechi-CYTB-595F	ACCCTAACCCGATTCTTCGC	this study
Proechi-CYTB-923R	GAGCGTAGAATTGCGTATGC	this study

[a] Custom primers were named according to their approximate location in an alignment of CYTB and tRNA-Glu sequences extracted from whole mitochondrial genome sequences in GenBank: NC039550 (*Proechimys steerei*) and NC039370 (*P. quadruplicatus*).

APPENDIX 3

SPECIMENS OF OECOMYS SEQUENCED FOR CYTOCHROME B

Species	Voucher[a]	Field no.	Locality (abbreviated)[b]	GenBank	Source
bicolor (N)	MVZ 200956*	JUR 566	BR: Amazonas, Colocação Vira-Volta (3.28°S, 66.23°W)	PP001501	J.L. Patton lab
bicolor (N)	ROM 105519*	F37752	EC: Orellana, 35 km S Pompeya Sur (0.63°S, 76.47°W)	PP001502	this study
bicolor (N)	ROM 105597*	F37840	EC: Orellana, 35 km S Pompeya Sur (0.63°S, 76.47°W)	PP001503	this study
bicolor (N)	ROM 105660*	F37905	EC: Orellana, 35 km S Pompeya Sur (0.63°S, 76.47°W)	PP001504	this study
bicolor (N)	ROM 104505*	F37351	EC: Orellana, 42 km S Pompeya Sur (0.68°S, 76.43°W)	PP001505	this study
bicolor (N)	ROM 118911*	F41922	EC: Orellana, 42 km S Pompeya Sur (0.68°S, 76.43°W)	PP001506	this study
bicolor (N)	TTU 84901*	TK104129	EC: Pastaza, 5 km E Puyo (1.73°S, 78.00°W)	PP001507	this study
bicolor (N)	TTU 85228*	TK104456	EC: Pastaza, 5 km E Puyo (1.73°S, 78.00°W)	PP001508	this study
bicolor (N)	MVZ 154988*	JLP 7341	PE: Amazonas, Huampami (4.47°S, 78.17°W)	PP001509	J.L. Patton lab
bicolor (N)	MVZ 154990*	JLP 7354	PE: Amazonas, Huampami (4.47°S, 78.17°W)	PP001510	J.L. Patton lab
bicolor (N)	MVZ 154991*	JLP 7360	PE: Amazonas, Huampami (4.47°S, 78.17°W)	PP001511	J.L. Patton lab
bicolor (N)	MVZ 154992*	JLP 7373	PE: Amazonas, Huampami (4.47°S, 78.17°W)	PP001512	J.L. Patton lab
bicolor (N)	MVZ 154997*	JLP 7618	PE: Amazonas, Huampami (4.47°S, 78.17°W)	PP001513	J.L. Patton lab
bicolor (N)	MVZ 154999*	JLP 7645	PE: Amazonas, Huampami (4.47°S, 78.17°W)	PP001514	J.L. Patton lab
bicolor (N)	MVZ 155001*	JLP 7690	PE: Amazonas, Huampami (4.47°S, 78.17°W)	PP001515	J.L. Patton lab
bicolor (N)	TTU 100834*	TK73027	PE: Loreto, 25 km S Iquitos (3.97°S, 73.42°W)	PP001516	this study
bicolor (N)	TTU 98621*	TK73046	PE: Loreto, 25 km S Iquitos (3.97°S, 73.42°W)	PP001517	this study
bicolor (N)	TTU 98829*	TK73532	PE: Loreto, 25 km S Iquitos (3.97°S, 73.42°W)	PP001518	this study
bicolor (N)	MUSM 17571*	LAC 392	PE: Loreto, Collpa Salvador (2.63°S, 75.15°W)	MG824904	MUSM project[c]
bicolor (N)	MUSM 17638	LAC 459	PE: Loreto, Collpa Salvador (2.63°S, 75.15°W)	MG824906	MUSM project[c]
bicolor (N)	MUSM 16000*	JAA 238	PE: Loreto, Jenaro Herrera (4.92°S, 73.67°W)	MG824899	MUSM project[c]
bicolor (N)	MUSM [uncat]	PSV 232	PE: Loreto, Llanchama (3.87°S, 73.40°W)	MG824903	MUSM project[c]
bicolor (N)	MUSM [uncat]	PSV 214	PE: Loreto, Llanchama (3.87°S, 73.40°W)	MG824901	MUSM project[c]
bicolor (N)	MUSM 44979	KPB 1573	PE: Loreto, Nina Rumi (3.86°S, 73.39°W)	MG824890	MUSM project[c]
bicolor (N)	MUSM 45737*	VPT 4486	PE: Loreto, Nina Rumi (3.86°S, 73.39°W)	MG824892	MUSM project[c]
bicolor (N)	MUSM 45738*	VPT 4495	PE: Loreto, Nina Rumi (3.86°S, 73.39°W)	MG824894	MUSM project[c]

APPENDIX 3 continued

Species	Voucher[a]	Field no.	Locality (abbreviated)[b]	GenBank	Source
bicolor (N)	MUSM 45739*	PSV 27	PE: Loreto, Nina Rumi (3.86°S, 73.39°W)	MG824895	MUSM project[c]
bicolor (N)	MUSM 45740*	VPT 4474	PE: Loreto, Nina Rumi (3.86°S, 73.39°W)	MG824909	MUSM project[c]
bicolor (N)	MUSM 45741*	VPT 4494	PE: Loreto, Nina Rumi (3.86°S, 73.39°W)	MG824910	MUSM project[c]
bicolor (N)	MUSM 45742*	VPT 4491	PE: Loreto, Nina Rumi (3.86°S, 73.39°W)	MG824893	MUSM project[c]
bicolor (N)	MUSM 45743*	PSV 31	PE: Loreto, Nina Rumi (3.86°S, 73.39°W)	MG824896	MUSM project[c]
bicolor (N)	AMNH 272674*	RSV 2046	PE: Loreto, Nuevo San Juan (5.25°S, 73.17°W)	PP001519	this study
bicolor (N)	MUSM 13315*	RSV 2070	PE: Loreto, Nuevo San Juan (5.25°S, 73.17°W)	PP001520	this study
bicolor (N)	MUSM 13316*	RSV 2099	PE: Loreto, Nuevo San Juan (5.25°S, 73.17°W)	PP001521	this study
bicolor (N)	MUSM 43188*	MDO 656	PE: Loreto, Pachacutec (4.99°S, 77.43°W)	MG824905	MUSM project[c]
bicolor (N)	FMNH 203674	PMV 2371	PE: San Martín, Tingana (5.91°S, 77.11°W)	PP001522	this study
bicolor (S)	MVZ 200958*	MNFS 1260	BR: Acre, Igarapé Porongaba (8.67°S, 72.78°W)	PP001523	J.L. Patton lab
bicolor (S)	MVZ 200959*	MNFS 1261	BR: Acre, Igarapé Porongaba (8.67°S, 72.78°W)	PP001524	J.L. Patton lab
bicolor (S)	MVZ 200963*	MNFS 1679	BR: Acre, Nova Vida (8.37°S, 72.82°W)	PP001525	J.L. Patton lab
bicolor (S)	MVZ 200882*	MNFS 1333	BR: Acre, opposite Igarapé Porongaba (8.67°S, 72.78°W)	PP001526	J.L. Patton lab
bicolor (S)	MVZ 200962*	MNFS 1499	BR: Acre, Sobral (8.37°S, 72.82°W)	PP001527	J.L. Patton lab
bicolor (S)	MVZ 200884*	JLP 15777	BR: Amazonas, Barro Vermelho (6.47°S, 68.77°W)	PP001528	J.L. Patton lab
bicolor (S)	MVZ 200964*	MNFS 749	BR: Amazonas, Barro Vermelho (6.47°S, 68.77°W)	PP001529	J.L. Patton lab
bicolor (S)	MVZ 200966*	JLP 15414	BR: Amazonas, Nova Empresa (6.80°S, 70.73°W)	PP001530	J.L. Patton lab
bicolor (S)	MVZ 200967*	JLP 15433	BR: Amazonas, Nova Empresa (6.80°S, 70.73°W)	PP001531	J.L. Patton lab
bicolor (S)	MVZ 200897*	MNFS 651	BR: Amazonas, Sacado (6.75°S, 70.85°W)	PP001532	J.L. Patton lab
bicolor (S)	MVZ 200971*	MNFS 652	BR: Amazonas, Sacado (6.75°S, 70.85°W)	PP001533	J.L. Patton lab
bicolor (S)	KU 144302*	CAS 686	PE: Madre de Dios, Cusco Amazónico (12.55°S, 69.05°W)	PP001534	J.L. Patton lab
bicolor (S)	KU 144304*	CAS 701	PE: Madre de Dios, Cusco Amazónico (12.55°S, 69.05°W)	PP001535	this study
bicolor (S)	KU 144305*	CAS 721	PE: Madre de Dios, Cusco Amazónico (12.55°S, 69.05°W)	PP001536	this study
bicolor (S)	KU 144314*	NW 609	PE: Madre de Dios, Cusco Amazónico (12.55°S, 69.05°W)	PP001537	J.L. Patton lab
bicolor (S)	KU 144322*	RMT 3926	PE: Madre de Dios, Cusco Amazónico (12.55°S, 69.05°W)	PP001538	J.L. Patton lab
bicolor (S)	KU 144325*	RMT 3934	PE: Madre de Dios, Cusco Amazónico (12.55°S, 69.05°W)	PP001539	this study
bicolor (S)	KU 144327*	NW 692	PE: Madre de Dios, Cusco Amazónico (12.55°S, 69.05°W)	PP001540	J.L. Patton lab

APPENDIX 3 *continued*

Species	Voucher[a]	Field no.	Locality (abbreviated)[b]	GenBank	Source
galvez (N)	ROM 105985*	F40237	EC: Orellana, 66 km S Pompeya Sur (0.81°S, 76.40°W)	PP001541	this study
galvez (N)	ROM 105986*	F40238	EC: Orellana, 66 km S Pompeya Sur (0.81°S, 76.40°W)	PP001542	this study
galvez (N)	ROM 105224*	F37543	EC: Orellana, 38 km S Pompeya Sur (0.66°S, 76.45°W)	PP001543	this study
galvez (N)	ROM 118868*	F41879	EC: Orellana, 42 km S Pompeya Sur (0.68°S, 76.43°W)	PP001544	this study
galvez (N)	ROM 105321*	F37649	EC: Orellana, 76 km S Pompeya Sur (0.83°S, 76.33°W)	PP001545	this study
galvez (N)	KU 158192*	NW 832	PE: Loreto, San Jacinto (2.32°S, 75.87°W)	PP001546	this study
galvez (S)	MVZ 200948*	MNFS 1250	BR: Acre, Igarapé Porongaba (8.67°S, 72.78°W)	PP001547	J.L. Patton lab
galvez (S)	MVZ 200955*	JLP 15425	BR: Amazonas, Penedo (6.83°S, 70.75°W)	PP001548	J.L. Patton lab
galvez (S)	AMNH 276720*	MVC 363	PE: Loreto, Jenaro Herrera (4.92°S, 73.67°W)	PP001549	this study
galvez (S)	MUSM 23819*	JAA 866	PE: Loreto, Jenaro Herrera (4.92°S, 73.67°W)	PP001550	this study
galvez (S)	AMNH 273122*	DWF 542	PE: Loreto, Nuevo San Juan (5.25°S, 73.17°W)	PP001551	this study
galvez (S)	MUSM 13320*	RSV 2023	PE: Loreto, Nuevo San Juan (5.25°S, 73.17°W)	PP001552	J.L. Patton lab
galvez (S)	MUSM 15336*	DWF 634	PE: Loreto, Nuevo San Juan (5.25°S, 73.17°W)	PP001553	this study
makampi	MUSM 15335*	DWF 730	PE: Loreto, Nuevo San Juan (5.25°S, 73.17°W)	PP001554	this study
nanus	MVZ 200906*	JUR 480	BR: Amazonas, Colocação Vira-Volta (3.28°S, 66.23°W)	PP001555	J.L. Patton lab
nanus	MVZ 200905*	JUR 354	BR: Amazonas, Lago Vai-Quem-Quer (3.32°S, 66.02°W)	PP001556	J.L. Patton lab
nanus	MVZ 200904*	JLP 15675	BR: Amazonas, Seringal Condor (6.75°S, 70.85°W)	PP001557	J.L. Patton lab
nanus	AMNH 276713*	JAA 864	PE: Loreto, Jenaro Herrera (4.92°S, 73.67°W)	PP001558	this study
nanus	MUSM 16001*	JAA 294	PE: Loreto, Jenaro Herrera (4.92°S, 73.67°W)	MG824900	MUSM project[c]
nanus	MUSM 23814*	JAA 835	PE: Loreto, Jenaro Herrera (4.92°S, 73.67°W)	PP001559	this study
nanus	MUSM 23815*	JAA 842	PE: Loreto, Jenaro Herrera (4.92°S, 73.67°W)	PP001560	this study
osgoodi	FMNH 175097*	SS 2171	PE: Cusco, Consuelo (13.02°S, 71.49°W)	PP001561	this study
"*paricola*"	ROM 104473*	F37313	EC: Orellana, 38 km S Pompeya Sur (0.66°S, 76.45°W)	PP001562	this study
"*paricola*"	ROM 106213	F40426	EC: Orellana, 38 km S Pompeya Sur (0.66°S, 76.45°W)	PP001563	this study
"*paricola*"	TTU 98907*	TK73722	PE: Loreto, 25 km S Iquitos (3.97°S, 73.42°W)	PP001564	this study
"*paricola*"	TTU 101252*	TK75156	PE: Loreto, 25 km S Iquitos (3.97°S, 73.42°W)	PP001565	this study
"*paricola*"	MUSM [uncat]	PSV 241	PE: Loreto, Llanchama (3.87°S, 73.40°W)	MG824902	MUSM project[c]
"*paricola*"	MUSM 44977	VPT 4439	PE: Loreto, Llanchama (3.87°S, 73.40°W)	MG824908	MUSM project[c]

APPENDIX 3 continued

Species	Voucher[a]	Field no.	Locality (abbreviated)[b]	GenBank	Source
"paricola"	MUSM 44978	KPB 1666	PE: Loreto, Llanchama (3.87°S, 73.40°W)	MG824891	MUSM project[c]
"paricola"	MUSM 44980*	KPB 1619	PE: Loreto, Llanchama (3.87°S, 73.40°W)	MG824911	MUSM project[c]
"paricola"	MUSM 45736	PSV 73	PE: Loreto, Llanchama (3.87°S, 73.40°W)	MG824897	MUSM project[c]
"paricola"	KU 158190*	NW 827	PE: Loreto, San Jacinto (2.32°S, 75.87°W)	PP001566	this study
roberti (A)	MVZ 200908*	MNFS 725	BR: Amazonas, Barro Vermelho (6.47°S, 68.77°W)	PP001567	J.L. Patton lab
roberti (A)	MVZ 200907*	MNFS 955	BR: Amazonas, Boa Esperança (6.53°S, 68.92°W)	PP001568	J.L. Patton lab
roberti (A)	MVZ 200909*	JLP 16033	BR: Amazonas, Boa Esperança (6.53°S, 68.92°W)	PP001569	J.L. Patton lab
roberti (A)	MVZ 200910*	MNFS 948	BR: Amazonas, Boa Esperança (6.53°S, 68.92°W)	PP001570	J.L. Patton lab
roberti (A)	MVZ 200912*	JUR 532	BR: Amazonas, Colocação Vira-Volta (3.28°S, 66.23°W)	PP001571	J.L. Patton lab
roberti (A)	MVZ 200927*	MNFS 681	BR: Amazonas, Jainu (6.47°S, 68.77°W)	PP001572	J.L. Patton lab
roberti (A)	MVZ 200928*	MNFS 692	BR: Amazonas, Jainu (6.47°S, 68.77°W)	PP001573	J.L. Patton lab
roberti (A)	MVZ 200917*	JLP 15402	BR: Amazonas, Nova Empresa (6.80°S, 70.73°W)	PP001574	J.L. Patton lab
roberti (A)	MVZ 200918*	JLP 15404	BR: Amazonas, Nova Empresa (6.80°S, 70.73°W)	PP001575	J.L. Patton lab
roberti (A)	MVZ 200947*	JLP 15241	BR: Amazonas, Penedo (6.83°S, 70.75°W)	PP001576	J.L. Patton lab
roberti (A)	MVZ 200934*	MNFS 577	BR: Amazonas, Sacado (6.75°S, 70.85°W)	PP001577	J.L. Patton lab
roberti (A)	MVZ 200935*	MNFS 578	BR: Amazonas, Sacado (6.75°S, 70.85°W)	PP001578	J.L. Patton lab
roberti (A)	MVZ 200915*	MNFS 537	BR: Amazonas, Seringal Condor (6.75°S, 70.85°W)	PP001579	J.L. Patton lab
roberti (A)	INPA 4193	MNFS 2018	BR: Amazonas, Tambor (2.22°S, 62.43°W)	PP001580	J.L. Patton lab
roberti (A)	INPA 4207	MNFS 2029	BR: Amazonas, Tambor (2.22°S, 62.43°W)	PP001581	J.L. Patton lab
roberti (A)	KU 144333*	CAS 712	PE: Madre de Dios, Cusco Amazónico (12.55°S, 69.05°W)	PP001582	J.L. Patton lab
roberti (A)	KU 144335*	NW 696	PE: Madre de Dios, Cusco Amazónico (12.55°S, 69.05°W)	PP001583	J.L. Patton lab
roberti (A)	KU 144336*	RMT 3955	PE: Madre de Dios, Cusco Amazónico (12.55°S, 69.05°W)	PP001584	this study
roberti (A)	KU 144338*	NW 742	PE: Madre de Dios, Cusco Amazónico (12.55°S, 69.05°W)	PP001585	this study
roberti (B)	MVZ 153528*	JLP 7251	PE: Amazonas, Huampami (4.47°S, 78.17°W)	PP001586	J.L. Patton lab
roberti (B)	MVZ 155005*	JLP 7357	PE: Amazonas, Huampami (4.47°S, 78.17°W)	PP001587	J.L. Patton lab
roberti (B)	TTU 98797*	TK73464	PE: Loreto, 25 km S Iquitos (3.97°S, 73.42°W)	PP001588	this study
roberti (B)	MUSM 17631*	LAC 452	PE: Loreto, Collpa Salvador (2.63°S, 75.15°W)	MG824917	MUSM project[c]
roberti (B)	MUSM 17685*	LAC 506	PE: Loreto, Collpa Salvador (2.63°S, 75.15°W)	MG824918	MUSM project[c]

APPENDIX 3 continued

Species	Voucher[a]	Field no.	Locality (abbreviated)[b]	GenBank	Source
roberti (B)	MUSM 44981*	VPT 4403	PE: Loreto, Nina Rumi (3.86°S, 73.39°W)	MG824912	MUSM project[c]
roberti (B)	MUSM 44982*	KPB 1575	PE: Loreto, Nina Rumi (3.86°S, 73.39°W)	MG824914	MUSM project[c]
roberti (B)	MUSM 44983*	KPB 1580	PE: Loreto, Nina Rumi (3.86°S, 73.39°W)	MG824915	MUSM project[c]
roberti (B)	MUSM 44984*	VPT 4414	PE: Loreto, Nina Rumi (3.86°S, 73.39°W)	MG824913	MUSM project[c]
roberti (B)	MUSM 16424*	EV 1141	PE: Loreto, Ullpayacu (4.58°S, 76.60°W)	MG824916	MUSM project[c]
roberti (C)	AMNH 273112*	DWF 518	PE: Loreto, Nuevo San Juan (5.25°S, 73.17°W)	PP001589	this study
roberti (C)	AMNH 273119*	DWF 533	PE: Loreto, Nuevo San Juan (5.25°S, 73.17°W)	PP001590	this study
roberti (C)	AMNH 276701*	JAA 846	PE: Loreto, Jenaro Herrera (4.92°S, 73.67°W)	PP001591	this study
roberti (C)	MUSM 15340*	DWF 461	PE: Loreto, Nuevo San Juan (5.25°S, 73.17°W)	PP001592	this study
superans	MVZ 200945*	MNFS 846	BR: Amazonas, Altamira (6.58°S, 68.90°W)	PP001593	J.L. Patton lab
superans	MVZ 200944*	JLP 15517	BR: Amazonas, Penedo (6.83°S, 70.75°W)	PP001594	J.L. Patton lab
superans	ROM 106144*	F40402	EC: Orellana, 18 km S Pompeya Sur (0.55°S, 76.52°W)	PP001595	this study
superans	ROM 118851*	F41862	EC: Orellana, 38 km S Pompeya Sur (0.66°S, 76.45°W)	PP001596	this study
superans	TTU 84945*	TKI04173	EC: Pastaza, 5 km E Puyo (1.73°S, 78.00°W)	PP001597	this study
superans	MVZ 155004*	JLP 7441	PE: Amazonas, Huampami (4.47°S, 78.17°W)	PP001598	J.L. Patton lab
superans	MVZ 155006*	JLP 7619	PE: Amazonas, Huampami (4.47°S, 78.17°W)	PP001599	J.L. Patton lab
superans	MVZ 155008*	JLP 7655	PE: Amazonas, Huampami (4.47°S, 78.17°W)	PP001600	J.L. Patton lab
superans	MVZ 155012*	JLP 7808	PE: Amazonas, Huampami (4.47°S, 78.17°W)	PP001601	J.L. Patton lab
superans	FMNH 175099*	BDP 4090	PE: Cusco, Consuelo (13.02°S, 71.49°W)	PP001602	this study
superans	MVZ 166698*	JLP 10909	PE: Madre de Dios, Hacienda Erika (12.85°S, 71.39°W)	PP001603	J.L. Patton lab
superans	UMMZ 160546	PM 4901	PE: Madre de Dios, Hacienda Erika (12.85°S, 71.39°W)	PP001604	J.L. Patton lab
superans	UMMZ 160547	PM 4915	PE: Madre de Dios, Hacienda Erika (12.85°S, 71.39°W)	PP001605	J.L. Patton lab
superans	KU 144332*	NW 510	PE: Madre de Dios, Cusco Amazónico (12.55°S, 69.05°W)	PP001606	J.L. Patton lab
sp	ROM 118895*	F41906	EC: Orellana, 42 km S Pompeya Sur (0.68°S, 76.43°W)	PP001607	this study
sp	MVZ 172649	JLP 13452	PE: Junín, 10 km WSW San Ramón (11.17°S, 75.43°W)	PP001608	J.L. Patton lab
sp	MUSM 43189*	MDO 678	PE: Loreto, Pachacutec (4.99°S, 77.43°W)	MG824907	MUSM project[c]
sp	MUSM 11013	JLM 132	PE: Pasco, Yanahuanca (10.04°S, 75.56°W)	MG824898	MUSM project[c]
sp	FMNH 175093*	SS 2194	PE: Cusco, Consuelo (13.02°S, 71.49°W)	PP001609	this study

APPENDIX 3 *continued*

Species	Voucher[a]	Field no.	Locality (abbreviated)[b]	GenBank	Source
sp	FMNH 172269*	SS 2047	PE: Cusco, San Pedro (13.05°S, 71.55°W)	PP001610	this study
sp	FMNH 170599*	BDP 3858	PE: Cusco, Suecia (13.10°S, 71.57°W)	PP001611	this study
sp	FMNH 170604*	BDP 3880	PE: Cusco, Suecia (13.10°S, 71.57°W)	PP001612	this study
sp	FMNH 170595*	SS 1804	PE: Madre de Dios, near Shintuya (12.67°S, 71.27°W)	PP001613	this study
sp	UMMZ 160550	PM 5031	PE: Madre de Dios, near Shintuya (12.68°S, 71.25°W)	PP001614	this study

[a] See Materials and Methods for institutional abbreviations. Specimens examined by R.S.V. to confirm taxonomic identifications are marked with an asterisk (*).

[b] Country abbreviations: BR, Brazil; EC, Ecuador; PE, Peru.

[c] "Caracterización molecular de roedores reservorios de enfermedades emergentes en la región amazónica y modelamiento de su distribución para la identificación de áreas de alto riesgo: caso hantavirus."

APPENDIX 4

SPECIMENS OF *PROECHIMYS* SEQUENCED FOR CYTOCHROME *B*

Species	Voucher[a]	Field no.	Locality[b]	GenBank	Source
brevicauda	MUSM 22358	MV 970001	San Pedro, right bank Río Blanco	PP001615	J.L. Patton lab
brevicauda	MUSM 22359	MV 970004	San Pedro, right bank Río Blanco	PP001616	J.L. Patton lab
brevicauda	MVZ 198475*	MV 970006	San Pedro, right bank Río Blanco	MG932501	J.L. Patton lab
brevicauda	MUSM 22352	MV 970091	San Pedro, right bank Río Blanco	PP001617	J.L. Patton lab
brevicauda	MUSM 22353	MV 970092	San Pedro, right bank Río Blanco	PP001618	J.L. Patton lab
brevicauda	MUSM 22354	MV 970093	San Pedro, right bank Río Blanco	PP001619	J.L. Patton lab
brevicauda	MUSM 13337*	RSV 2050	Nuevo San Juan, Río Gálvez	PP001620	J.L. Patton lab
brevicauda	AMNH 272698*	RSV 2092	Nuevo San Juan, Río Gálvez	PP001621	J.L. Patton lab
brevicauda	MUSM 13338*	RSV 2120	Nuevo San Juan, Río Gálvez	PP001622	J.L. Patton lab
cuvieri	[unknown]	MV 970010	San Pedro, right bank Río Blanco	MG932510	J.L. Patton lab
cuvieri	MUSM 22376	MV 970021	San Pedro, right bank Río Blanco	PP001623	J.L. Patton lab
cuvieri	UF 30788*	MV 970034	San Pedro, right bank Río Blanco	MG932512	J.L. Patton lab
cuvieri	MUSM 22398	MV 970070	La Colmena, Quebrada La Colmena	PP001624	J.L. Patton lab
cuvieri	MVZ 198511*	MV 970080	La Colmena, Quebrada La Colmena	MG932509	J.L. Patton lab
kulinae	MUSM 22409	MV 970015	San Pedro, right bank Río Blanco	PP001625	J.L. Patton lab
kulinae	MUSM 22410	MV 970016	San Pedro, right bank Río Blanco	PP001626	J.L. Patton lab
kulinae	MUSM 22364	MV 970028	San Pedro, right bank Río Blanco	PP001627	J.L. Patton lab
kulinae	MVZ 198489*	MV 970031	San Pedro, right bank Río Blanco	PP001628	J.L. Patton lab
kulinae	[unknown]	MV 970059	La Colmena, Quebrada La Colmena	MG932513	J.L. Patton lab
kulinae	[unknown]	MV 970078	La Colmena, Quebrada La Colmena	MG932514	J.L. Patton lab
kulinae	[unknown]	MV 970079	La Colmena, Quebrada La Colmena	MG932515	J.L. Patton lab
kulinae	MUSM 13340	RSV 2026	Nuevo San Juan, Río Gálvez	PP001629	J.L. Patton lab
kulinae	AMNH 272714*	RSV 2132	Nuevo San Juan, Río Gálvez	PP001630	J.L. Patton lab
quadruplicatus	MVZ 198518*	MV 970098	El Chino, left bank Río Tahuayo	PP001631	J.L. Patton lab
quadruplicatus	MUSM 22515	MV 970099	El Chino, left bank Río Tahuayo	PP001632	J.L. Patton lab
quadruplicatus	MUSM 22516	MV 970101	El Chino, left bank Río Tahuayo	PP001633	J.L. Patton lab
quadruplicatus	MUSM 22517	MV 970102	El Chino, left bank Río Tahuayo	PP001634	J.L. Patton lab
quadruplicatus	MUSM 22518	MV 970104	El Chino, left bank Río Tahuayo	PP001635	J.L. Patton lab
quadruplicatus	MUSM 22529	MV 970117	El Chino, left bank Río Tahuayo	PP001636	J.L. Patton lab
quadruplicatus	MVZ 198534*	MV 970122	El Chino, left bank Río Tahuayo	MG932530	J.L. Patton lab
simonsi	MUSM 22419	MV 970035	San Pedro, right bank Río Blanco	PP001637	J.L. Patton lab
simonsi	MUSM 22545	MV 970038	San Pedro, right bank Río Blanco	MG932544	J.L. Patton lab
simonsi	MVZ 198498*	MV 970047	San Pedro, right bank Río Blanco	MG932545	J.L. Patton lab
simonsi	MUSM 13345	RSV 2027	Nuevo San Juan, Río Gálvez	PP001638	J.L. Patton lab
simonsi	AMNH 272677	RSV 2051	Nuevo San Juan, Río Gálvez	PP001639	J.L. Patton lab
simonsi	MUSM 13342*	RSV 2076	Nuevo San Juan, Río Gálvez	PP001640	J.L. Patton lab
steerei	MUSM 11278*	DWF 147	Nuevo San Juan, Río Gálvez	PP001641	this study
steerei	MUSM 11279*	DWF 155	Nuevo San Juan, Río Gálvez	PP001642	this study

[a] See Materials and Methods for institutional abbreviations. Specimens examined by R.S.V. to confirm taxonomic identifications are marked with an asterisk (*).
[b] See appendix 1 for geographic coordinates.

APPENDIX 5

Additional Rodent Species Expected to
Occur in the Yavarí-Ucayali Interfluve

Daptomys peruviensis: This semiaquatic mouse belongs to the sigmodontine cricetid tribe ichthyomyine and was formerly known as *Neusticomys peruviensis* (after Voss, 1988), but current binomial usage follows Salazar-Bravo et al. (2023). Recently collected specimens have been reported from localities immediately north and south of the Yavarí-Ucayali interfluve (Pacheco et al., 2020), where it doubtless also occurs. Species of *Daptomys* are seldom collected except in pitfalls or in traplines set along the margins of small streams, methods that have yet to be used intensively in our region.

Neacomys carceleni: This taxon, formerly treated as a synonym of *N. spinosus* (e.g., by Weksler and Bonvicino, 2015a), was recognized as a valid subspecies of *N. amoenus* by Hurtado and Pacheco (2017) and as a valid species by Brito et al. (2021). Hurtado and Pacheco (2017) listed four specimens that they identified as *N. a. carceleni* from Jenaro Herrera (MUSM 23812, 23813, 15993, 15994), but all have subsequently been reidentified as *N. aletheia* (see Sánchez-Vendizú et al., 2018; this report).[46] Although it is plausible that *N. carceleni* occurs in the Yavarí-Ucayali interfluve, we have not seen any specimens from our region.

Oecomys superans: This is a widespread species of semiarboreal oryzomyine known from multiple localities north and south of our region (Carleton and Musser, 2015: map 216). There is some evidence to suggest that it occurs in secondary vegetation (Patton et al., 2000), a habitat that was perhaps undersampled by trapping in the Yavarí-Ucayali interfluve.

Rhipidomys leucodactylus: This arboreal rat belongs to the sigmodontine cricetid tribe Thomasomyini. It is known from multiple localities south of our region (e.g., along the Rio Juruá in western Brazil; Patton et al., 2000) and north of our region (e.g., in northern Loreto; Sánchez-Vendizú et al., 2021). Although elusive (species of *Rhipidomys* are notoriously difficult to trap or shoot in tall forest), it does not appear to be a habitat specialist and almost certainly occurs in the Yavarí-Ucayali interfluve.

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[46] *Neacomys aletheia* corresponds to the "upriver clade" of *N. minutus* in Sánchez-Vendizú et al. (2018).

APPENDIX 6

Amazonian Distributions of Rodents from the Yavarí-Ucayali Interfluvial Fauna

	Amazonian quadrants[a]				
	NE	NW	SE	SW	References
Sciurillus pusillus	X	X	X	X	Vivo & Carmignotto, 2015
Sciurus pachecoi				X	this report
Sciurus pyrrhinus		X		X	Vivo & Carmignotto, 2015[b]
Sciurus spadiceus		X	X	X	Vivo & Carmignotto, 2015
Sciurus flaviventer		X		X	Vivo & Carmignotto, 2015
Amphinectomys savamis		X		X	Chiquito & Percequillo, 2017[b]
Euryoryzomys macconnelli	X	X	X	X	Percequillo, 2015a
Holochilus nanus	X	X	X	X	Prado, 2021b
Hylaeamys perenensis		X		X	Percequillo, 2015b
Hylaeamys yunganus	X	X	X	X	Percequillo, 2015b
Neacomys aletheia				X	Semedo et al., 2021[b]
Neacomys musseri				X	Sánchez-Vendizú et al., 2018[b]
Nectomys apicalis		X		X	Bonvicino & Weksler, 2015[b]
Nectomys rattus	X	?	X	X	Bonvicino & Weksler, 2015[c]
Oecomys bicolor	X	X	X	X	Carleton & Musser, 2015
Oecomys nanus				X	this report
Oecomys makampi				X	this report
Oecomys galvez		X		X	this report
Oecomys roberti	X	X	X	X	this report
Oligoryzomys microtis		X	?	X	Weksler & Bonvicino, 2015b
Scolomys melanops		X		X	this report
Scolomys ucayalensis		X		X	Patton, 2015a
Hydrochoerus hydrochaeris	X	X	X	X	Dunnum, 2015
Cuniculus paca	X	X	X	X	Patton, 2015b
Dasyprocta fuliginosa	X	X	X	X	Patton & Emmons, 2015a
Myoprocta pratti		X		X	Patton & Emmons, 2015a
Dinomys branickii		X		X	Patton, 2015c[d]
Coendou ichillus		X		X	Gregory et al., 2015[b]
Coendou longicaudatus	X	X	X	X	Voss, 2015
Dactylomys dactylinus	X	X	X	X	Emmons et al., 2015b
Isothrix bistriata		X		X	Emmons & Patton, 2015a
Makalata "species 5"				X	Miranda et al., 2021
Mesomys hispidus	X	X	X	X	Patton & Emmons, 2015b
Toromys rhipidurus		X		X	Emmons & Fabre, 2018
Proechimys brevicauda		X		X	Patton & Leite, 2015
Proechimys cuvieri	X	X	X	X	Patton & Leite, 2015

APPENDIX 6 *continued*

	Amazonian quadrants[a]				References
	NE	NW	SE	SW	
Proechimys kulinae				X	Patton & Leite, 2015
Proechimys quadruplicatus	X	X		X	Patton & Leite, 2015[b]
Proechimys simonsi		X		X	Patton & Leite, 2015
Proechimys steerei		X		X	Patton & Leite, 2015

[a] Abbreviations (see fig. 58): NE, northeast (north of the lower Amazon and east of the Rio Negro); NW, northwest (north of the upper Amazon and west of the Rio Negro); SE, southeast (south of the lower Amazon and east of the Rio Madeira); SW, southwest (south of the upper Amazon and west of the Rio Madeira).

[b] With additional information summarized in this report.

[c] Although the range map for *Nectomys rattus* in Bonvicino and Weksler (2015) is shaded to include much of northwestern Amazonia, we have not seen any specimens from eastern Ecuador, eastern Colombia, or north of the Amazon in Peru. The single specimen of *N. rattus* mapped by those authors in eastern Colombia (AMNH 136324) is misidentified: it is unambiguously an example of *N. apicalis.* The type locality of *N. rattus* is on the right bank of the upper Rio Negro, but there seems to be no compelling evidence that it occurs elsewhere in northwestern Amazonia.

[d] Patton's (2015c) range map for *Dinomys branickii* does not include northwestern Amazonia, but a specimen collected in 1943 near Miraflores (1°25′N, 72°13′W; DMA, 1988) on the Río Vaupés in eastern Colombia, is in the Museum of Comparative Zoology (MCZ 43486).